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Assessment of Growth Response and Patterns of Biomass Allocation by *Panicum hemitomon* Schultes: Implications for Thick-mat Floating Marsh Creation and Restoration

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Assessment of Growth Response and Patterns of Biomass Allocation by Panicum
hemitomon Schultes: Implications for Thick-mat Floating Marsh Creation and
Restoration

A Dissertation

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

Doctor of Philosophy
in
Conservation Biology

by

C. Ellery Mayence

BA, University of North Carolina at Chapel Hill, 1999
MEM, Duke University, 2003

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Abstract

I carried out several large, manipulative greenhouse and controlled-setting experiments to elucidate Panicum hemitomon growth response as influenced by environmental conditions associated with restoring thick-mat floating marsh. Initially, Panicum hemitomon growth response was assessed in conjunction with manipulated nutrient availability and hydrology. Next, I assessed Panicum hemitomon growth response in conjunction with a suite of substrate and mat or containment materials. Finally, I evaluated Panicum hemitomon growth response, as well as overall created floating marsh vegetated development, using both a multi-species planting approach and a suite of Panicum hemitomon establishment techniques.

All partitions of Panicum hemitomon biomass (shoot, rhizome, and root material) were enhanced under nitrogen, and to a lesser extent, phosphorous enrichment. Saturated (not inundated) hydrologic conditions were most conducive for robust growth by all partitions of Panicum hemitomon biomass. Substrate and mat or containment materials had a significant effect on Panicum hemitomon vigor, with peat and peat-containing blended substrate materials being most conducive for vigorous Panicum hemitomon growth. Duralast coconut fiber was the most suitable mat or containment material based not only on measures of plant vigor, but also for reasons associated with strength and stability, as well as buoyancy. The combination of Panicum hemitomon and Ludwigia peploides was superior to any other multi-species treatment tested. Ludwigia peploides was highly resilient to transplanting, grew vigorously in a lateral fashion, produced significantly more biomass than any other secondary species, and enhanced overall mat buoyancy, all key metrics regarding successful floating marsh restoration. Equally as important, the large amount of biomass attained by Ludwigia peploides was not totally at the expense of vigorous Panicum hemitomon growth. With respect to establishment technique, the

positive response of Panicum hemitomom rhizome growth to humic acid amendment warrants further study.

This research generated data that not only advance the body of general ecological knowledge pertaining to Panicum hemitomom, the dominant macrophyte of thick-mat floating marsh, but equally as important, data that are likely to augment or enhance the creation and restoration of this important freshwater marsh type.

Keywords: Panicum hemitomom, floating marsh, biomass allocation, multi-species approach

Chapter 1

Introduction

Project impetus

The impetus for this research was the need to develop a protocol for creating and restoring thick-mat floating marsh in coastal Louisiana. Thick-mat floating marsh is regarded as an important constituent of the freshwater wetland mosaic in coastal Louisiana, and over the past several decades its conversion to either less structurally-sound floating marsh types, or in some locations to open water, has incited significant concern among both ecologists and resource managers. To ameliorate these losses, an effort to devise a protocol specifically tailored to the restoration of thick-mat floating marsh was launched. Much of the research described herein attempts to elucidate those critical data and knowledge voids that not only existed prior to project initiation, but are deemed crucial for successful thick-mat floating marsh restoration.

With respect to wetland restoration, Sasser et al. (1993) recognized that floating marshes differ considerably from more typical attached or emergent marshes. They also noted that when recommendations are made regarding wetland restoration science, that guidelines generally make few or no references to floating marshes, but rather for attached marshes that are clearly different. According to Sasser et al. (1993), floating marsh development, and therefore restoration, must be focused on building an organic substrate that is held together by plant roots. Furthermore, they suggested that strategies for marsh development, or in this case marsh restoration, should include a buoyant substrate, appropriate vegetation, protection from physical disturbance, exclusion of herbivores, and ultimately, an effective fertilization regime (Sasser et al. 1993). Importantly, nearly 15 years later, not only are these same provisions still

relevant, but many of them have yet to be elucidated to a point sufficient for the development of a protocol for restoring floating marshes. The dissertation research described herein, and the larger collaborative project of which it is part, directly target several of these provisions to further elucidate their role in floating marsh formation. My intent for this body of work was to advance what is known about plant growth response in a floating marsh context, and by doing so, contribute to the development of protocol for restoring floating marsh.

Project background

Wetland ecosystems are the dominant landscape feature throughout coastal and inland portions of Louisiana. Depending on type and location, key ecosystem services afforded by wetland ecosystems may include flood mitigation, water quality management, biogeochemical cycling, and naturalness-related aesthetic values (Mitsch and Gosselink 2001). Additionally, wetlands provide critical habitat for a rich body of fauna, with many, most notably those in marine settings, serving as essential nursery grounds for numerous fisheries of high recreational and commercial importance (Turner 1977 and 1992; Rosas and Reed 1993; Peterson and Turner 1994; Mitsch and Gosselink 2001). Many cultural aspects important to Louisiana, but particularly important to bayou culture, are also largely dependent on the presence of coastal wetlands (Hallowell 2001; Streever 2001; Tidwell 2003). Considering the services and associated benefits afforded by these ecosystems, there is interest on a variety of fronts to better understand their ecology, and in areas where they have been degraded or lost, there is both a heightened interest and an imminent need to further develop restoration strategies and techniques.

Causes of wetland loss in Louisiana have been studied extensively and are well documented (Craig et al. 1979; Gagliano et al. 1981; Evers et al. 1992; Britsch and Dunbar 1996; Turner 1997). Causes stem from both anthropogenic activities and non-anthropogenic

processes including, but not limited to, delta evolution, altered regional hydrology, subsidence and associated sea-level rise, tropical cyclone activity, oil and gas exploration and extraction, and residential and commercial development. The result of these activities and processes is the exceptionally high rate of wetland loss experienced in Louisiana, ranging from 60 to 100 km² yr⁻¹ (Britsch and Kemp 1990; Penland et al. 1990; Britsch and Dunbar 1996; Turner 1997). In unusually active years with respect to tropical cyclone activity, rates of wetland loss may greatly exceed the 60 to 100 km² yr⁻¹ average, as occurred in 2005 when an estimated 217 km² of coastal wetlands were lost (USGS 2006). Consequently, the long-term sustainability of many wetlands of the deltaic region has been questioned.

Louisiana's non-fresh coastal habitats, such as brackish and saline marshes, and barrier islands, have received the most restoration attention (CWPPRA 1993; Steyer and Llewellyn 2000). Comparatively, floating marshes have only recently received attention, although as alluded to earlier, there has been interest regarding their restoration from the scientific community for quite some time (Sasser et al. 1993). In a recent study, Sasser et al. (2005) assessed the feasibility of reverting thin-mat floating marsh to a more structurally-sound floating marsh type with successful results (Thin-Mat Floating Marsh Enhancement Demonstration Project TE-36). Although encouraging, employing such an approach would not be possible in areas where floating marsh degradation has been so severe that open water now exists. To restore floating marsh in such areas, it became clear that a more comprehensive and integrated approach was needed, although information regarding how to proceed was incomplete. This project (LA-05-Floating Marsh Creation Demonstration Project) was funded as a means for assessing the feasibility of restoring floating marsh, notably thick-mat floating marsh, in such settings.

Project structure

The Coastal Wetlands Planning, Protection, and Restoration Act (CWPPRA), House Document 646, 101st Congress, provides federal funds to be used for devising and implementing projects that create, protect, restore, and enhance coastal wetlands of the United States. The federally-administered CWPPRA mandates that costs associated with such projects be shared by governmental agencies at both the state and federal levels. For the LA-05-Floating Marsh Creation Demonstration Project, the United States Department of Agriculture – Natural Resources Conservation Service (USDA-NRCS) partnered with the Louisiana Department of Natural Resources (LaDNR). Research duties were divided among the Coastal Ecology Institute at Louisiana State University, the Coastal Plant Ecology Laboratory at the University of Louisiana at Lafayette, and the Department of Biological Sciences at the University of New Orleans.

Floating marsh distribution, formation, and ecology

Floating marshes in Louisiana (Image 1.1, top panel) are confined to freshwater areas (salinity < 2 ppt.) east of the Atchafalaya River, but west of the Mississippi River (Russell 1942; Evers et al. 1992; Sasser 1994; Sasser et al. 1996; Visser et al. 1999). In more extensive geographical terms, floating marshes are not confined to Louisiana, or even to North America. Other forms of floating or quaking marshes have been described in Florida (Hunt 1943), the Amazon delta of Brazil (Junk 1970; Junk and Piedale 1997), the Sudd region of the upper Nile drainage in Sudan (Migahid 1947), the Okavango delta in Botswana (Ellery et al. 1990), portions of eastern Russia (Zhulidov et al. 1997), and various river systems in other parts of Europe and Asia (Moore and Bellamy 1974; Zimmerli 1988; Myint and Maung 2000; Su and Jassby 2000).

First described in the 1940s (Russell 1942; O'Neil 1949), floating marshes in Louisiana have since been classified into several different types (Figure 1.1, bottom panel) as a result of general field reconnaissance and numerous field and controlled-setting studies. These studies include assessments of floating marsh distribution, vegetative composition, hydrology, and substrate characteristics (O'Neil 1942; Russell 1949; Evers et al. 1992; Sasser 1994; Sasser et al. 1995a and 1995b; Sasser et al. 1996; Visser et al. 1999), buoyancy-related qualities (Swarzenski et al. 1991; Holm et al. 2000; Fisher 2003), associated nutrient regimes (DeLaune et al. 1986; Sasser et al. 1991), and most recently, the restoration potential of thin-mat floating marsh (Sasser et al. 2005). Of the different floating marsh types classified by Sasser et al. (1994), thick-mat floating marsh (Figure 1.1, bottom image, Class I) is considered to be the most structurally sound and buoyant. Thick mat floating marsh also exhibits year-round buoyancy, whereas other types tend to be buoyant only during the height of the growing season.

Like other types of floating marsh, thick-mat is composed of the aboveground shoot biomass, the associated living and dead rhizome and root biomass, and partially decomposed organic matter or peat. However, what distinguishes it from other types is not solely its highly-buoyant nature, but the thickness of the underlying root mat, which can reach and exceed 0.5 m, and the fact that it is almost always dominated by Panicum hemitomon (Sasser et al. 1995b). Panicum hemitomon Schultes (maidencane), a clonal monocotyledonous grass found in freshwater-dominated areas throughout the northern Gulf of Mexico region (Godfrey and Wooten 1979a), produces the rhizome and root biomass that is crucial for thick-mat floating marsh structural integrity and buoyancy. In these marshes, oxygen-limited and oligotrophic conditions depress rates of decomposition, enhancing the accumulation of organic matter, and as a result, the thickening of the root mat. The peat-dominated substrates exhibit low bulk

densities compared to substrates with greater mineral content, further contributing to the buoyancy of these marshes (Delaune et al. 1986; Sasser 1994; Sasser et al. 1995a).

All indications suggest that floating marsh formation occurs in the upper portions of the Mississippi River deltaic plain in the later stages of the delta cycle when distributary courses are no longer, or much less, hydraulically active (Sasser et al. 1995a). In these areas not only are sediments often highly unconsolidated, but water depths are generally too great for the establishment of emergent vegetation. Such physical conditions are not considered constraints on floating marsh formation however. Two dominant theories are generally accepted with respect to floating marsh formation, with several other theories recognized, but considered less likely responsible for large-scale formation (Sasser 1994). The edge expansion theory, first proposed by Russell (1942), involves the lateral growth of vegetation from the marsh edge into open water, or areas otherwise unvegetated. This lateral advancement is achieved by Panicum hemitomon, and to a greater extent, by laterally-growing species (i.e., edge specialists) that couple high relative growth rates with buoyant stems. The second theory, proposed by O'Neil (1949) and referred to as the popping cork theory, is likely more responsible for larger areas of formation because of its association with deltaic subsidence and increased marsh water levels. Under this scenario, formation begins with vegetation rooted on a mesic or minimally-flooded surface. Subsidence stemming from sediment dewatering and consolidation leads to increased marsh water levels, which collectively force the vegetated mat to detach from the sediment surface and float. The degree to which the detached marsh floats depends on several factors, although substrate characteristics and plant species composition appear most important (Sasser et al. 1995a and 1995b). Gaseous compounds, either leaked from plant roots or generated by resident microbial communities, are also suspected to contribute to marsh buoyancy, as has been documented for other floating or quaking wetlands (Hogg and Wein 1988a and 1988b).

However, this phenomenon has not been thoroughly researched, and is therefore not fully understood with respect to thick-mat floating marsh.

Importantly, and representing the main reason for restoration, the extent of Panicum hemitomon-dominated thick-mat floating marsh has declined in recent decades (Sasser 1986; Evers 1992, Visser et al. 1999). The largest shift occurred over the period from 1960 to 1990 when thick-mat floating marsh declined by as much as 50% in some areas, particularly southwestern Terrebonne Basin (Evers et al. 1992; Visser et al. 1999). Interestingly, and over many of the same areas, Eleocharis baldwinii (Torr.) Chapman-dominated thin-mat floating marsh increased nearly by as much as 50% (Visser et al. 1999). Potential causes of this shift include grazing by Myocastor coypus L. (nutria), altered hydrology in the form of salt water intrusion and increased wave action, tropical cyclone activity, and in some cases, eutrophication (Sasser et al. 2005). Regardless of cause, such shifts have lead some to consider the notion of a successional relationship between thick-mat and thin-mat floating marsh, particularly the degradation or conversion of thick-mat to thin-mat (i.e., the conversion of type – I to type – IV as classified in Figure 1.1; Sasser et al. 1986 and 1996; Visser et al. 1999). Considering the amount of loss incurred to date, and the likelihood for future losses, developing a protocol for thick-mat floating marsh restoration is a high priority.

Crucial data and knowledge voids

Whereas the degradation and fragmentation of thick-mat floating marsh has been well documented, information crucial to successfully developing a protocol for its restoration has not been thoroughly research, and is therefore lacking. This was the case even though it has been demonstrated that Panicum hemitomon exhibits a broad ecological niche (salinity tolerance not included), is easily propagated from cuttings and rhizome fragments, and responds well to experimental manipulation (Hester et al. 1988; Pezeshki et al. 2000; Kirkman and Sharitz 2003;

Willis and Hester 2004). Despite these studies, there is still ambiguity in the scientific literature with respect to Panicum hemitomon growth response and patterns of biomass allocation as influenced by hydrologic regime. Moreover, there has been relatively little scientific investigation of Panicum hemitomon growth response under different levels of nutrient availability, an important knowledge void considering the concern over eutrophication in coastal Louisiana. Furthermore, and with particular relevance to floating marsh restoration, there is essentially no information detailing Panicum hemitomon growth response as influenced by substrate material, much less for different mat materials that are needed to contain the substrate material. Although there has been general interest for some time to evaluate the potential benefits of using laterally-growing plant species for restoration purposes, there is relatively little scientific information regarding growth response data or morphological attributes of candidate species for such endeavors. The same is also true with respect to means for enhancing Panicum hemitomon establishment, or avenues for greater restoration cost-effectiveness.

Clearly then, a significant amount of crucial information is lacking with for devising a protocol for restoring thick-mat floating marsh, information that needs to be elucidated prior to attempting large-scale restoration, hence the objectives and rationale of the research described herein. Each experimental chapter that follows is designed to elucidate specific ecophysiological aspects of Panicum hemitomon growth response and patterns of biomass allocation as influenced by: nutrient and hydrologic regime (Chapter 2); substrate and mat or containment materials (Chapter 3); or species-level competitive interactions in a multi-species setting, combined with a cursory evaluation of different Panicum hemitomon establishment techniques (Chapter 4). The concluding chapter is designed to synthesize these experiments via a discussion on the extent to which they advance what is known about ecophysiological aspects

of Panicum hemitomom growth response and patterns of biomass allocation, as well as how this information can be used to make informed decisions for restoring, and in some instances better managing, floating marshes.

Chapter 2

The Effect of Manipulated Nutrient Availability and Hydrology on Growth Response and Patterns of Biomass Allocation by Panicum hemitomon

Introduction

Primary objectives

The objectives of the experiments described in this chapter were to elucidate Panicum hemitomon growth response and patterns of biomass allocation in conjunction with environmental conditions, specifically nutrient availability and hydrologic regime, that are considered important for successful thick-mat floating marsh restoration. Because robust belowground production is vital to creating and sustaining a structurally-sound floating marsh, and the detailed scientific data required to achieve such objectives were lacking, documenting specific attributes of rhizome and root growth (i.e., rhizome biomass and length, root biomass, root specific gravity, and root:shoot ratio) are key to developing a protocol that will result in successful floating marsh restoration. In addition, these experiments allowed for other, important growth-related parameters, such as total aboveground biomass and photosynthetic nitrogen-use efficiency, to be assessed. Apart from the strict restoration-oriented objectives, I also expected this research to further elucidate ecophysiological attributes of Panicum hemitomon, at least under the conditions employed for these studies.

Background

Wetland plants require specific anatomical and physiological adaptations for tolerating stress associated with hydrologic inundation and reduced (hypoxic) soil conditions (Lambers et al. 1998; Cronk and Fennessey 2001). In terms of nutrient requirements and mechanisms of nutrient acquisition, wetland or flood-tolerant plants employ similar strategies to those of

terrestrial plants (Chapin 1980; Epstein and Bloom 2005). The governing effect of soil fertility on the relative allocation to above- and belowground components, as well as its influence on the morphology of these components, has received considerable scientific attention, particularly with respect to species representative of nutrient-poor versus nutrient-rich sites (Chapin 1980; Vitousek 1982; Boerner 1984; Iwasa and Roughgarden 1984; Vitousek and Matson 1984; Berendse 1994; Crawley 2005). Plants inhabiting nutrient-rich habitats typically have higher maximum relative growth rates, and become more robust, compared to individuals from stressful, nutrient-poor habitats (Parsons 1968; Chapin 1980; Grime and Hunt 1975; Lambers and Porter 1992). Species inhabiting nutrient-rich sites also tend to exhibit greater photosynthetic capacity, or rates of carbon dioxide assimilation (Pons et al. 1989; Mooney and Ehleringer 2005). It has been suggested that species from nutrient-poor habitats may invest more dry matter in roots, whereas species from nutrient-rich habitats may invest more in shoots (Brouwer 1963; Chapin 1980; Tilman 1988; Tilman and Cowan 1989; Fitter 2005). In more specific terms, many have suggested that plants allocate relatively less biomass to aboveground components, and more to belowground components, when nitrogen or phosphorous is limiting (Brouwer 1963 and 1983; Iwasa and Roughgarden 1984). Although such patterns of allocation may seem logical (i.e., increased allocation to roots should confer an advantage in capturing limited soil resources), there has not always been unanimous support in the ecological literature for such patterns. Elberse and Berendse (1993) found that species from nutrient-poor habitats allocated less dry matter to roots, and consequently more to shoots, than species from nutrient-rich habitats. They also suggested that the inherent morphology of roots and leaves, not solely the allocation to those components, seemed most clearly adapted to their respective habitats. It seems clear then that not only is there variability in patterns of biomass allocation as influenced by site fertility, but also a tendency for individuals of the same species to exhibit

phenotypic plasticity when grown under similar environmental conditions. Elucidating variation in allocation patterns, and determining the degree to which it is governed by local environmental conditions, was a key direction of this assessment of Panicum hemitomom growth response as applied to floating marsh restoration.

By investing in root structures, plants gain anchorage, as well as moisture and nutrient acquisition and uptake (de Kroon and Visser 2003). Several authors (Crick and Grime 1987, Campbell and Grime 1989, and Hutchings and de Kroon 1994) have found significant plasticity in root morphology in response to spatial and temporal variability in substrate fertility. These studies also suggested that plants from nutrient-poor habitats respond differently to nutrient enrichment compared to plants from nutrient-rich habitats, particularly whether root proliferation occurs locally in nutrient-rich patches, or by roots not associated with nutrient rich patches. Using the perennial grass Holcus lanatus L., Fransen and de Kroon (2001) observed greater relative root biomass in rich soil when growing in a split treatment with poor soil, as compared to plants grown under uniformly rich conditions. Plants grown in a heterogeneous treatment with similar nutrient patch characteristics, but overall poorer soil, did not exhibit comparable root growth (Fransen and de Kroon (2001). Drew (1975), working with Hordeum vulgare L., observed the proliferation of lateral roots in nutrient rich patches, whereas Linkhor et al. (2002) demonstrated using Arabidopsis thaliana L. (Heynh.), that enhanced root growth in nutrient-rich patches came at the expense of decreased root growth in nutrient-poor patches. In an earlier study, Williamson et al. (2001), also employing Aradibopsis thaliana, concluded that phosphorous enrichment lead to decreased lateral root growth, but increased primary root growth. Similar conclusions were reached by Zhang et al. (1996) under nitrogen enrichment. Based on the preceding findings, it seems clear that growth responses, and to a lesser degree growth strategies, are both largely species and site specific.

The influence of site hydrology on overall plant performance is dependent on species-specific adaptations and the frequency and duration of flooding events (Gambrell et al. 1991; Lambers et al. 1998). Oxygen deficiency is the predominant change that occurs with the onset of flooding because the diffusion of oxygen in water is 10^{-4} of that in air (Armstrong 1982; Epstein and Bloom 2005). In addition to enhanced aerenchyma formation (Evans 2004), flooding is associated with increased adventitious root formation (Kludze and Delaune 1996; Laurentius 1996), decreased root mass and overall root growth rates (de Kroon and Visser 2003), and increased rates of stem elongation (Ridge 1987; Vartapetian and Jackson 1997). Even for wetland-adapted species like Panicum hemitomon, such stressors likely influence belowground plant response, an important consideration given the role of rhizome and root biomass in forming the support structure (i.e., root mat) of thick-mat floating marsh.

Thick-mat floating marsh is generally considered a nutrient-limited wetland ecosystem (DeLaune et al. 1986; Sasser et al. 1995b) resulting from nutrient loss to the free-water zone under the root mat, and to immobilization of nitrogen and phosphorous by resident microbial communities (Delaune et al. 1986; Sasser et al. 1991). The exception occurs during infrequent and short duration flooding events that temporarily enrich surrounding waters. In light of this, an important objective of this study was to determine whether Panicum hemitomon biomass allocation patterns would shift in response to nutrient enrichment, and if so, would such a shift favor shoot biomass or rhizome and root biomass. In an effort to increase the relevance of this research, eutrophic nutrient loading rates were chosen because many wetlands in Louisiana, including Panicum hemitomon-dominated floating marsh downstream of river diversions, are experiencing eutrophic conditions. It was equally as important to identify shifts in allocation patterns as influenced by both saturated and inundated hydrologic conditions. Elucidating individual and interactive effects of these two parameters on Panicum hemitomon growth

response and patterns of biomass allocation was viewed as the initial step for developing a protocol for floating marsh restoration. Importantly, adopting Panicum hemitomon growth response data from other studies was not considered a viable option because floating marsh differs too greatly from more typical attached marshes, wetland types that nearly all previous studies were partial to.

The main objectives of this study were to:

- (1) Elucidate individual and interactive effects of manipulated nitrogen and phosphorous availability and hydrology on Panicum hemitomon growth response and patterns of biomass allocation.
- (2) Interpret these findings within a thick-mat floating marsh restoration context.

The main hypotheses of this study were:

Overarching hypothesis:

Panicum hemitomon growth and patterns of biomass allocation will vary significantly according to manipulations of nutrient availability and hydrology.

Key hypotheses:

1. Under enriched, as compared to non-enriched nitrogen and phosphorous availability, Panicum hemitomon will exhibit:
 - A. Increased above- and belowground production, increased total rhizome length, but a decreased root:shoot ratio
 - B. Greater tissue nitrogen content, rates of photosynthesis, but lower photosynthetic nitrogen use-efficiency
2. In inundated, as compared to saturated hydrologic conditions, Panicum hemitomon will exhibit:
 - A. Increased mean stem height (and aboveground production), but decreased rhizome and root production
 - B. Lower (more buoyant) root specific gravity

Materials and Methods

Experimental design

This Materials and Methods section describes two separate experiments, but they are referred to as phase – I and phase – II because the latter was conducted primarily as a result of the former being destroyed by flooding associated with Hurricane Katrina. Despite their similarities, there are differences in the two experimental designs. Phase – I (Image 2.1, top panel) was initiated in July of 2004, and partially salvaged in October of 2005 after thirteen months of growth (for all practical purposes this experiment was terminated in August of 2005 in conjunction with the landfall of Hurricane Katrina). Because of its early termination, several key analyses were not performed, particularly assessments of live root morphology. Phase – II (Image 2.1, bottom panel) was implemented in March of 2006, and harvested intact at peak standing crop in June of 2006 after four months of growth. Phase – II was conducted largely to execute those key analyses not performed in phase – I. Phase – II also allowed for a more applied, or comprehensive, evaluation of Panicum hemitomon growth response and patterns of biomass allocation because it was designed explicitly with floating marsh restoration in mind.

Phase – I employed a 3 x 3 x 2 completely cross-classified factorial design with 3 levels of nitrogen loading (2.5, 25, and 50 g N m⁻² yr⁻¹) in the form NH₄-NO₃, 3 levels of phosphorous loading (2, 5, and 10 g P m⁻² yr⁻¹) in the form CaPO₄, and 2 hydrologic regimes [0 cm of flooding (or saturated) and 15 cm of flooding (or inundated)], each replicated once across 5 blocks for a total of 90 experimental units (n = 90). Phase – II employed a 2 x 2 x 2 completely cross-classified factorial design with 2 levels of nitrogen loading (25 and 50 g N m⁻² yr⁻¹) in the form NH₄-NO₃, 2 levels of phosphorous loading (5 and 10 g P m⁻² yr⁻¹) in the form CaPO₄, and 2 hydrologic regimes [0 cm of flooding (or saturated) and 15 cm of flooding (or inundated)], each replicated once across 5 blocks for a total of 40 experimental units (n = 40).

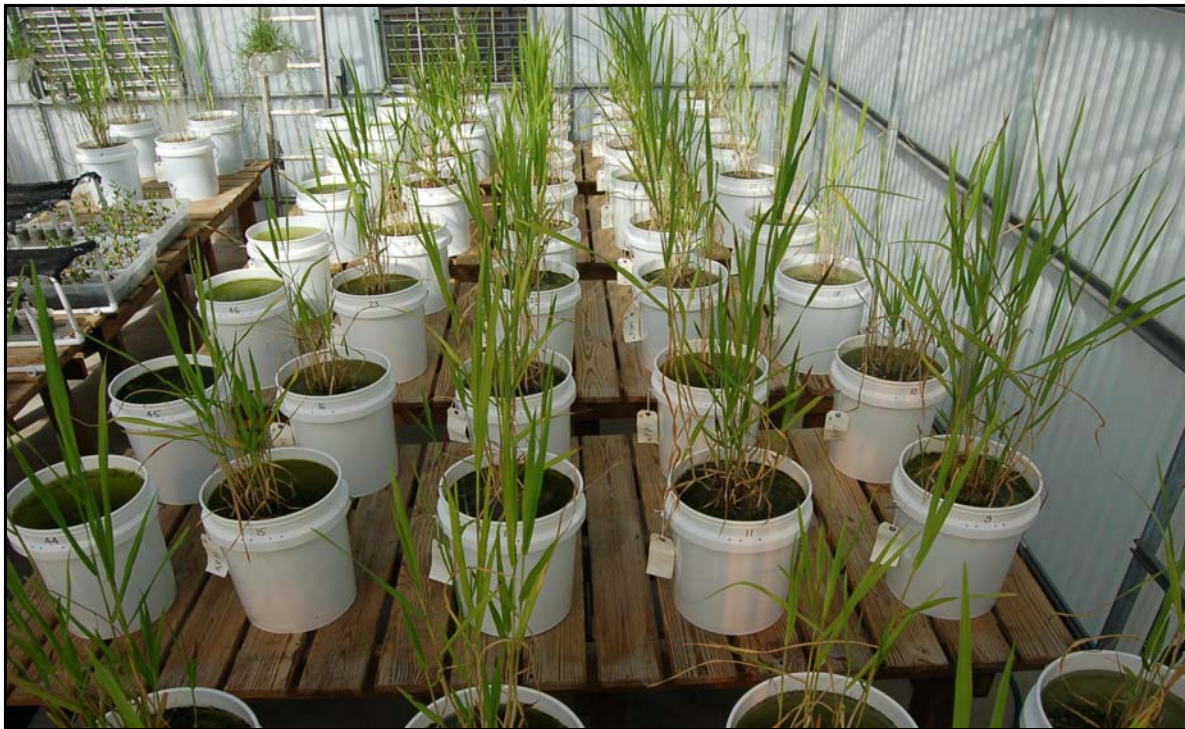


Image 2.1. View of the phase – 1 study (top image) in September of 2004, six weeks after initiation (twelve months prior to destruction by Hurricane Katrina), and the phase – II study (bottom image) in April of 2006, eight weeks after initiation.

The phase – II study did not include the lowest nitrogen and phosphorous loading rates because of negligible growth associated with these treatments in phase – I. Nitrogen and phosphorous loading rates for both phases were based on mean annual nitrogen and phosphorous outflow loading rates from the Caernarvon diversion, Caernarvon, LA. In particular, the mid-level loading rates for phase – I ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $5 \text{ g P m}^{-2} \text{ yr}^{-1}$ respectively), and the low-level loading rates for phase – II ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $5 \text{ g P m}^{-2} \text{ yr}^{-1}$ respectively), were based on peak values in the range of mean annual nitrogen and phosphorous loading rates ($8.9 - 23.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $0.9 - 2.0 \text{ g P m}^{-2} \text{ yr}^{-1}$ respectively) as reported by Lane et al. (1999). For phase – I, these mean rates were bracketed by a one-tenth strength (0.1X) and a two-fold strength (2X) nitrogen loading rate, and by a one-half strength (0.5X) and a two-fold strength (2X) phosphorous loading rate, to simulate the variability exhibited by nutrient concentrations in the diversion outflow. For the phase – II study, mean rates were bracketed by two-fold strength (2X) nitrogen and phosphorous loading rates. In both phases, nitrogen and phosphorous additions were administered weekly, whereas Hoagland's micronutrient solution (Hoagland and Arnon 1954) and other cations were administered monthly. Both phases were carried out in full-transmission glasshouse settings where daily temperatures ranged from $10 - 23^{\circ}\text{C}$ in winter to $23 - 44^{\circ}\text{C}$ in summer.

Panicum hemitomon was the only species employed in both experimental phases. Plant material for the phase – I study was purchased in the form of bare-root seedlings from a commercial nursery operation (Horticultural Systems, Palmdale, FL), whereas plant material for phase – II was harvested as root and rhizome stock from a single clone growing at the USDA Golden Meadow Plant Materials Center, Galliano, LA. Root and rhizome stock was transported back to the greenhouse facility at the University of New Orleans, and propagated for approximately six weeks in 10 cm plastic pots filled with enriched 18-6-12 (N-P-K respectively)

Miracle-Gro potting soil (Scotts Miracle-Gro Company, Marysville, OH). Mesic hydrologic conditions were maintained for the entirety of the propagation period.

The experimental set-up for the phase – I study is best described as hydroponic. Duralast coconut fiber (Duralast Products, Memphis, TN) served as both the substrate and mat or containment material. Two square 700 cm² layers of Duralast coconut fiber were fastened together with cable ties and planted with four plugs of Panicum hemitomom, one in each corner (referred to as a vegetated mat hereafter). All vegetated mats were maintained for the entirety of the experiment in rectangular, 72-L vessels filled to capacity with deionized water, with the desired hydrologic regime achieved by placing each mat on a pedestal fashioned from 10 cm diameter polyvinyl chloride (PVC) pipe. Note that pedestals were used to achieve the desired hydrologic regime because it was important for the volume of water in each experimental vessel to be uniform with respect to the nutrient regime. Set-up for the phase – II study involved the sandwiching of a 3 to 5 cm layer of ground sphagnum peat moss (Waupaca Northwoods LLC., Waupaca, WI), referred to as peat hereafter, between two circular 729 cm² layers of Duralast coconut fiber, also held together by cable ties. Each created mat was planted with a bare root plug of Panicum hemitomom, and maintained in a 19-L vessel for the entirety of the experiment. Deionized water was again used as the in phase – I study. Also as in phase – I, desired flooding depths were achieved using 10 cm diameter PVC pipe as pedestals. Prior to planting in both phases, all soil was washed from roots, and to avoid biased treatment effects, Panicum hemitomom plugs exhibiting statistically similar wet masses were chosen.

Because the phase – I study was destroyed prior to the final harvest, only the most important findings are included here. Moreover, and for comparative purposes, only those phase – I results associated with the nitrogen and phosphorous loading rates tested in phase – II have been included. Treatment conditions for the lowest nitrogen and phosphorous loading

rates for the phase – I study, particularly for inundated treatments, were such that many stems either perished or exhibited near negligible growth up until the destruction of the experiment.

Edaphic data

Substrate redox potential and interstitial pH were not assessed in the phase – I study because ecologically significant differences were not anticipated based on aspects of the experimental design (i.e., hydroponic conditions and monthly changing of vessel solutions). In contrast, substrate redox potential and interstitial pH for the phase – II study were measured twice over the course of the experiment. Substrate redox potential was measured using three platinum-tipped probes inserted into each vegetated mat to a depth of approximately 5 cm. Note that redox was measured within the vegetated mat, not in the water column beneath the mat. Probes were constructed according to methods described by Faulkner (1989), and brightened and calibrated prior to use. Upon insertion, probes were allowed to equilibrate for approximately 0.5 hours, after which readings were taken using a hand-held millivolt meter (Hanna model HI9025 pH/mV meter) and a KCL saturated calomel reference electrode. Each raw value was adjusted by +244 mV for the calomel reference electrode that was used (Faulkner 1989).

Interstitial pH was measured twice over the course of phase – II. Samples were withdrawn using an interstitial water sipper according to methods described by McKee et al. (1988), and measured using a hand-held Corning 313 pH/mV meter (Corning Instruments, Fairport, NY).

Shoot data

Cumulative stem height, the total height of all live stems emerging from a given vegetated mat, including rhizomes extending above the surface of the water with obvious leaf material, was measured monthly for both phase – I and II. Cumulative stem height is

considered an effective method for non-destructively tracking and assessing aboveground plant growth over time (Zedler 2001). Measuring cumulative stem height also allowed for the determination of total stem number, total stem height, and mean stem height.

Net CO₂ assimilation was measured at peak standing crop using a Li-Cor 6400 portable photosystem (Li-Cor, Lincoln, NE). Measurements were performed on two fully-expanded leaves, generally the second and third from the terminal leaf of each plant or vegetated mat. All measurements were performed under light-saturated conditions [$1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR)] with reference CO₂ levels set at 370 ppm. Each leaf on which photosynthetic measurements were performed was subsequently clipped and oven-dried at 60°C for approximately five days, or until a constant mass was attained. Each pair of leaves was then ground using a Wiley Mill so that carbon-hydrogen-nitrogen (CHN) analyses could be performed. The relationship between leaf area and leaf dry weight was determined on a separate subset of leaf samples. CHN results were used in conjunction with leaf mass:area ratios and photosynthetic results to determine leaf tissue nutrient content and plant photosynthetic nitrogen-use efficiency (PNUE).

Harvested biomass

After four months of growth for the phase – II study, all above- and belowground biomass (i.e., shoot, rhizome, and root biomass) was harvested. All shoot biomass emerging from each vegetated mat, as well as all rhizome biomass above the first node from which emergent roots were clearly visible, was considered aboveground biomass. Shoot biomass was not separated into live and dead components because all biomass was living at the time of harvest. All rhizome and root material below the first node from which emergent roots were clearly visible was considered belowground biomass. Belowground biomass was separated into either root or rhizome material, and all residual peat was thoroughly rinsed and passed through

a 1.5 mm sieve to account for all fine root material. Stem-borne adventitious roots associated with inundated treatments were separated from stems and included in the root metric for these treatments. All rhizome and root material was stored in plastic bags and refrigerated to minimize desiccation and/or rot prior to conducting morphological analyses. At the culmination of phase – II, but prior to drying, the length of all rhizome material was measured to determine the total rhizome length per vegetated mat. Rhizome length, serving as a surrogate for lateral spreading potential, was important here and in successive experiments, because Panicum hemitomom generally reproduces clonally, with rhizome growth representing the predominant means of growth. Apparently, Panicum hemitomom rarely produces seeds, and when it does, they often exhibit low viability (Hatch et al. 1999). Ultimately, all biomass was placed in paper bags and oven-dried at 60°C for approximately five days, or until a constant mass was attained.

Root morphological data

Root production was a key aspect of this research because of its vital role with respect to floating marsh mat structural integrity and buoyancy. Root systems associated with each vegetated mat were assessed non-destructively and destructively, as well as on individual root, and whole root-system levels (i.e., some analyses utilized entire root systems, whereas others utilized sub-samples of entire root systems).

Root specific gravity, the only belowground metric that was assessed in both phase – I and II, was measured prior to harvest according to those methods described by Burdick (1989). In all cases, it was determined on five root samples per treatment using between 0.05 and 0.10 g of freshly-harvested tissue. A representative sample of ten roots was obtained from each experimental treatment (not individual vegetated mat) and assigned a unique ID. A random number generator was then used to select five roots from these ten for analyses (no stem-borne adventitious roots were used for root specific gravity analyses). Root specific gravity

(RSG) was calculated using the formula: $RSG = R/(P + R - PR)$, where R = mass of roots, P = mass of water-filled pycnometer, and PR = mass of pycnometer with roots and water. Because the specific gravity of water is equal to 1.0, root tissue with a specific gravity less than 1.0 was considered buoyant, whereas a root specific gravity greater than 1.0 was not.

Total root volume for all experimental units in the phase – II study was determined at harvest using the entire root system of each vegetated mat, including stem-borne adventitious roots when present. This was achieved using an Epson 10000-XL high-resolution scanner, and the Pro-Version of Whin-RHIZO Root Imaging Software (Regent Instruments, Québec, Canada). As stipulated by the standard operating procedures for Whin-RHIZO, clean roots were placed in a transparent, water-filled tray and scanned. Importantly, depending on the amount of root biomass, as many as six separate scans were performed to quantify root volume for a given experimental unit. Each image was then digitized and analyzed using Whin-RHIZO software, with the resolution of the analysis set to a level determined by root morphology and operator preferences (i.e., fine-textured roots required greater resolution). All roots on which morphological analyses were conducted were accounted for when whole-plant root biomass and volume were assessed.

A collection of individual root morphological metrics was also quantified using Whin-RHIZO. These metrics included: root length, diameter, volume, and number of root tips. A representative sample of ten roots was obtained from each vegetated mat, and assigned a unique ID, noting that these were different sub-samples than those used for root specific gravity. From these ten, a random number generator was then used to select four roots per vegetated mat, but once replicates were accounted for (i.e., five per treatment), a total of twenty roots were analyzed per treatment.

Root length and volume per root diameter class, measured on the same lot of roots used to assess root morphometrics, but in this case using only five roots per treatment, were also determined using Whin-RHIZO. Both root length and volume per root diameter class were first quantified by classifying root diameter on the basis of 0.5 mm increments, and second by determining the proportion of either total root length, or total volume within each 0.5 mm diameter class. Diameter classifications for root length and volume were as follows: 0.0 – 0.49, 0.5 – 0.99, 1.0 – 1.49, 1.5 – 1.99, and 2.0 – 4.99 mm. Statistical analyses were performed only on intervals for which sufficient data were obtained.

Statistical analyses

SAS Version 9.1 (SAS Institute, Cary, NC) was used for all statistical analyses reported herein. All variables were evaluated independently to ensure that each clearly met the normality and heteroscedasticity assumptions associated with analysis of variance (ANOVA). A two-way ANOVA using the SAS PROC GLM procedure was used to test for differences in all non-sequentially measured variables. A multivariate repeated measures analysis of variance (MANOVA), also using the SAS PROC GLM procedure, was used to test for differences among sequentially measured variables. The MANOVA procedure is the preferred repeated-measures technique when multiple contrasts are performed on independent factors with two or more levels. A significance level of $\alpha = 0.05$ was used for all statistical tests unless specified otherwise. For tests of significance associated with MANOVA outputs, preference was given to Wilk's lambda when test of significance values did not differ. When differences did exist, preference was given to Pillai's trace because of its robustness to violations of assumptions (Kleinbaum et al. 1998; Scheiner and Gurevitch 2001). For post-hoc tests, only ecologically significant test results are included in the Results section. Other post-hoc tests, when performed, are reported in the Appendix.

Results

Edaphic data

Substrate redox for the phase – II study (Figure 2.1) decreased over time in nearly all treatments (Wilk's lambda: $F_{1,32} = 62.09$, $p < 0.0001$). Redox potentials were not significantly affected by nutrient enrichment, although values tended to be lower under nitrogen and phosphorous enrichment. In contrast, as evidenced by the change in values from March to May, redox potentials were significantly lower under saturated, as compared to inundated, hydrologic conditions (Wilk's lambda: $F_{1,32} = 7.64$, $p = 0.0094$). By the May sampling, reduced or mildly hypoxic redox potentials (i.e., values < 400 mV) were present in most treatments. The time by nutrient by hydrology interaction was not significant.

Interstitial pH for the phase – II study (Appendix, Figure 1) increased over time for all treatments (Wilk's lambda: $F_{1,32} = 59.98$, $p < 0.0001$). The rate of increase was not influenced by nutrient regime, but rather by hydrologic regime, with a significantly greater rate of pH increase observed for saturated, as compared to inundated, hydrologic conditions (Wilk's lambda: $F_{1,32} = 20.13$, $p < 0.0001$). The time by nutrient by hydrology interaction was not significant.

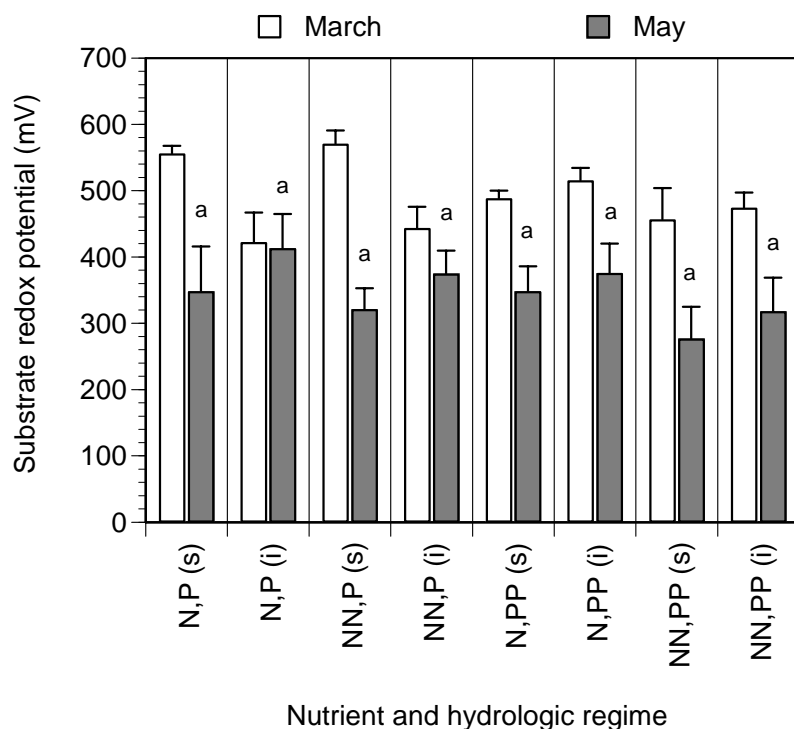


Figure 2.1. The effect of manipulated nutrient availability and hydrology on substrate redox potential for the phase – II study, measured in March and May. Treatment codes are as follows: N = low nitrogen; NN = high nitrogen; P = low phosphorous; PP = high phosphorous; s = saturated; i = inundated. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for May data only ($F_{7,32} = 0.81$, $p = 0.5839$).

Shoot data

Panicum hemitomom cumulative stem height for the phase – I study (Figure 2.2, top panel) increased over the period from July 2004 to July 2005, exhibiting a highly significant main effect of time (Wilk's lambda: $F_{3,30} = 73.62$, $p < 0.0001$). A significant time by nutrient interaction was also observed (Pillai's trace: $F_{9,96} = 4.78$, $p = 0.0052$), with plants receiving both enriched nitrogen and phosphorous exhibiting a greater rate of increase in stem height. At the final round of stem measurements (July 2005), this trend was still significant ($F_{7,32} = 20.17$, $p < 0.0001$). The time by hydrology interaction was not significant, nor was the time by nutrient by hydrology interaction.

Slightly different results were observed for the phase – II study (Figure 2.2, bottom panel), although cumulative stem height increased over time for nearly all treatments (Wilk's lambda: $F_{2,31} = 77.05$, $p < 0.0001$). The time by nutrient interaction was highly significant (Pillai's trace: $F_{6,64} = 3.45$, $p = 0.0052$), with nitrogen enrichment resulting in a greater rate of increase in cumulative stem height. The time by hydrology interaction was also highly significant (Wilk's lambda: $F_{2,31} = 9.53$, $p = 0.0006$), with saturated hydrologic conditions exhibiting greater rates of increase in cumulative stem height than inundated conditions. By the end of the study in June, cumulative stem heights associated with nitrogen enrichment, and to a lesser extent with saturated hydrologic conditions, were significantly greater than most other treatments ($F_{7,32} = 12.56$, $p < 0.0001$). The time by nutrient by hydrology interaction was not significant.

Panicum hemitomom total stem number, total stem height, and mean stem height for phase – I and II studies (Appendix, Table 1), all exhibited statistically significant treatment effects. Each stem metric was greater under nitrogen enrichment, with the effects of hydrology less clear.

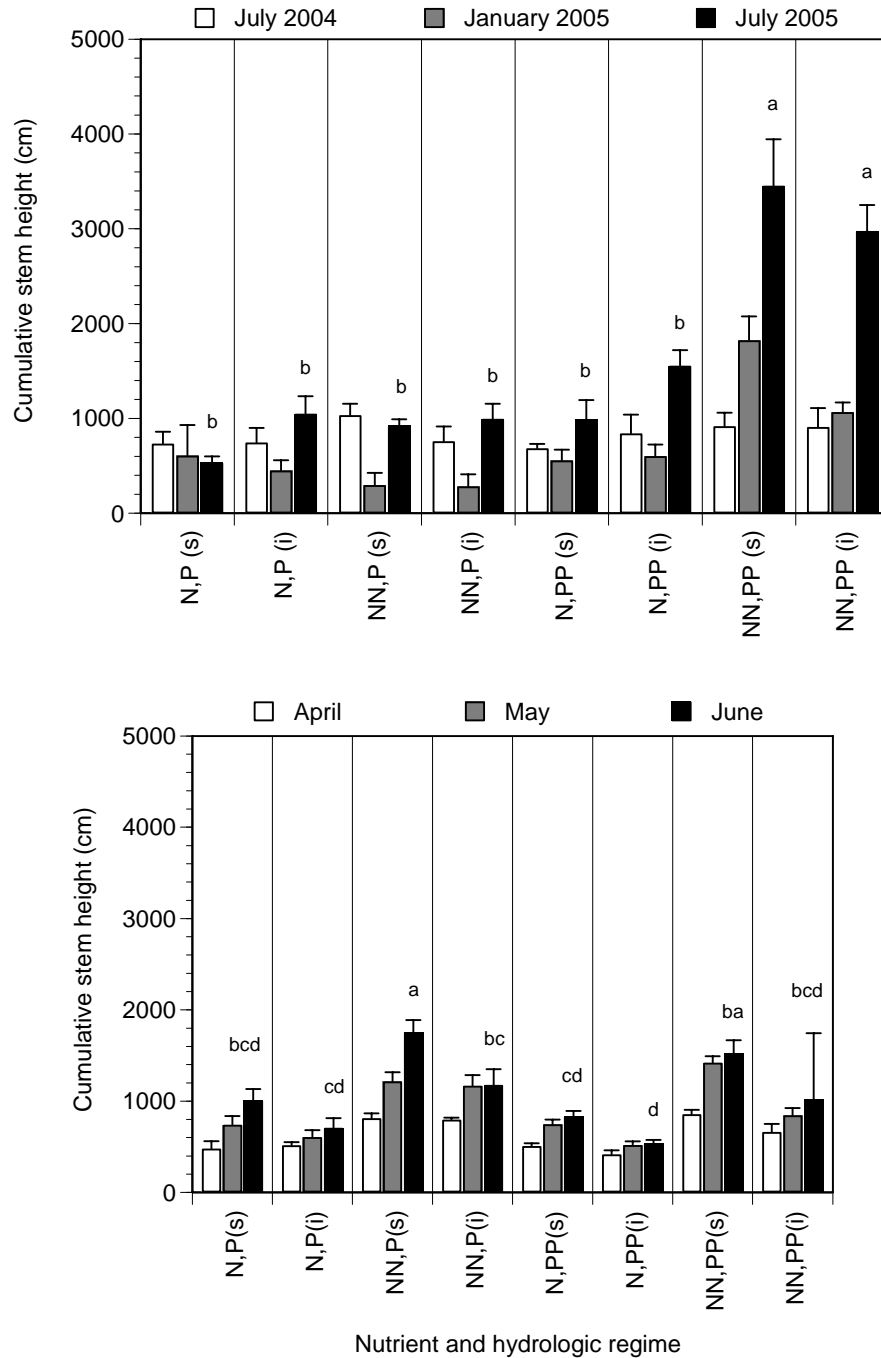


Figure 2.2. The effect of manipulated nutrient availability and hydrology on Panicum hemitomon cumulative stem height (cm) for phase – I (top panel) and phase – II (bottom panel), measured monthly over a twelve-month period for phase – I, and monthly over a four-month period for phase – II. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,P = high nitrogen and low phosphorous; N,PP = low nitrogen and high phosphorous; NN,PP = high nitrogen and high phosphorous; s = saturated; i = inundated. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for July 2005 (top panel; $F_{7,32} = 20.17$, $p < 0.0001$) and June data only (bottom panel; $F_{7,32} = 12.56$, $p < 0.0001$).

Panicum hemitomom tissue nitrogen content, net CO₂ assimilation, and PNUE for the phase – I study (Table 2.1, top portion), were relatively uniform across each factor and level, with no significant treatment effects observed. In contrast, tissue nitrogen content and net CO₂ assimilation for the phase – II study (Table 2.1, bottom portion) exhibited a significant effect of hydrology, with saturated conditions resulting in significantly greater tissue nitrogen content and net CO₂ assimilation than inundated conditions. The variability exhibited by these two factors did not significantly affect PNUE. Linear regression analyses of Panicum hemitomom PNUE as a factor of leaf tissue nitrogen content (Appendix, Table 2 and Figure 2) revealed no ecologically significant effects or trends in either study.

Table 2.1. *Panicum hemitomon* tissue nitrogen content (%), net CO₂ assimilation ($\mu\text{mol C m}^{-2} \text{ s}^{-1}$), and PNUE ($\mu\text{mol C g}^{-1} \text{ N s}^{-1}$) for both phase – I and II. Values are means \pm SE (n = 5).

<u>Phase – I</u>			
Treatment	Tissue nitrogen content (%)	Net CO ₂ assimilation ($\mu\text{mol C m}^{-2} \text{ s}^{-1}$)	PNUE ($\mu\text{mol C g}^{-1} \text{ N s}^{-1}$)
N,P (saturated)	1.6 \pm 0.07 ^a	27.4 \pm 5.20 ^a	24.1 \pm 5.84 ^a
N,P (inundated)	1.7 \pm 0.15 ^a	29.3 \pm 3.99 ^a	29.0 \pm 9.19 ^a
NN,P (saturated)	1.8 \pm 0.07 ^a	28.7 \pm 2.15 ^a	22.2 \pm 7.43 ^a
NN,P (inundated)	2.2 \pm 0.12 ^a	31.7 \pm 3.72 ^a	17.3 \pm 5.86 ^a
N,PP (saturated)	1.6 \pm 0.18 ^a	25.4 \pm 3.59 ^a	20.8 \pm 3.41 ^a
N,PP (inundated)	1.9 \pm 0.27 ^a	36.6 \pm 3.84 ^a	29.4 \pm 6.10 ^a
NN,PP (saturated)	1.8 \pm 0.25 ^a	26.0 \pm 3.42 ^a	32.9 \pm 4.91 ^a
NN,PP (inundated)	1.8 \pm 0.20 ^a	26.9 \pm 2.35 ^a	29.3 \pm 6.41 ^a
<i>F</i> – value (df 7,32)	1.07 ^{NS}	1.00 ^{NS}	0.70 ^{NS}
<u>Phase – II</u>			
Treatment	Tissue nitrogen content (%)	Net CO ₂ assimilation ($\mu\text{mol C m}^{-2} \text{ s}^{-1}$)	PNUE ($\mu\text{mol C g}^{-1} \text{ N s}^{-1}$)
N,P (saturated)	1.5 \pm 0.08 ^{ba}	10.4 \pm 0.82 ^{bac}	11.3 \pm 0.92 ^a
N,P (inundated)	1.1 \pm 0.08 ^b	7.3 \pm 0.73 ^c	10.9 \pm 1.03 ^a
NN,P (saturated)	1.5 \pm 0.05 ^{ba}	11.1 \pm 0.82 ^{ba}	11.7 \pm 0.97 ^a
NN,P (inundated)	1.3 \pm 0.10 ^{ba}	9.4 \pm 0.72 ^{bac}	11.4 \pm 0.47 ^a
N,PP (saturated)	1.4 \pm 0.11 ^{ba}	9.0 \pm 0.84 ^{bac}	10.1 \pm 0.85 ^a
N,PP (inundated)	1.1 \pm 0.06 ^b	7.0 \pm 0.88 ^c	10.1 \pm 1.52 ^a
NN,PP (saturated)	1.7 \pm 0.18 ^a	12.0 \pm 0.87 ^a	11.8 \pm 0.77 ^a
NN,PP (inundated)	1.3 \pm 0.07 ^{ba}	8.5 \pm 0.65 ^{bc}	10.6 \pm 0.65 ^a
<i>F</i> – value (df 7,32)	3.79 ^{**}	4.74 ^{**}	0.49 ^{NS}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Significant difference ($p < 0.01$); ^{NS} non-significant difference ($p > 0.05$)

Harvested biomass

In the phase – II study, Panicum hemitomon shoot biomass (Figure 2.3, top panel; Appendix, Table 3) was significantly greater under nitrogen enrichment ($F_{3,32} = 31.13$, $p = 0.0001$), and in saturated, as compared to inundated, hydrologic conditions ($F_{1,32} = 16.35$, $p = 0.0003$). Together, saturation (0 cm flooding) and nitrogen enrichment ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$) resulted in nearly a three-fold increase in shoot biomass as compared to the treatment group experiencing inundated (15 cm flooding) and non-enriched ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$) nitrogen conditions. Phosphorous enrichment had no noticeable effect on shoot biomass. The nutrient by hydrology interaction was not significant.

Although not as distinct as patterns observed for shoot biomass, Panicum hemitomon root biomass for the phase – II study (Figure 2.3, bottom panel; Appendix, Table 3) was significantly greater with nitrogen enrichment ($F_{3,32} = 8.64$, $p = 0.0002$), and in saturated, as compared to inundated, hydrologic conditions ($F_{1,32} = 119.88$, $p < 0.0001$). Saturation (0 cm flooding), and to a lesser extent, nitrogen enrichment ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$), resulted in significantly more root biomass as compared to inundation (15 cm flooding), and non-enriched ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$) nitrogen conditions. The nutrient by hydrology interaction, although only marginally significant ($F_{3,32} = 2.24$, $p = 0.0504$), is worth noting. As evident from post-hoc comparisons, root biomass responded more strongly to hydrologic regime than to nutrient treatment, whereas shoots exhibited responses of similar magnitude to both factors.

Although not assessed quantitatively, different patterns in root distribution were observed across the range of treatments employed here. Plants grown under nitrogen enrichment, and in saturated hydrologic conditions, exhibited more fine root biomass in the surface layers of the vegetated mat, and greater coarse root biomass at depth in the mat, and in the water column under the mat. In contrast, plants grown under non-enriched nutrient

conditions did not exhibit a noticeable pattern in root distribution. Moreover, all plants grown in inundated conditions exhibited stem-borne adventitious roots between the surface of the vegetated mat and the water line, with enriched nutrient conditions seeming to support greater adventitious rooting. In contrast, stem-borne adventitious roots were not observed for plants grown in saturated conditions.

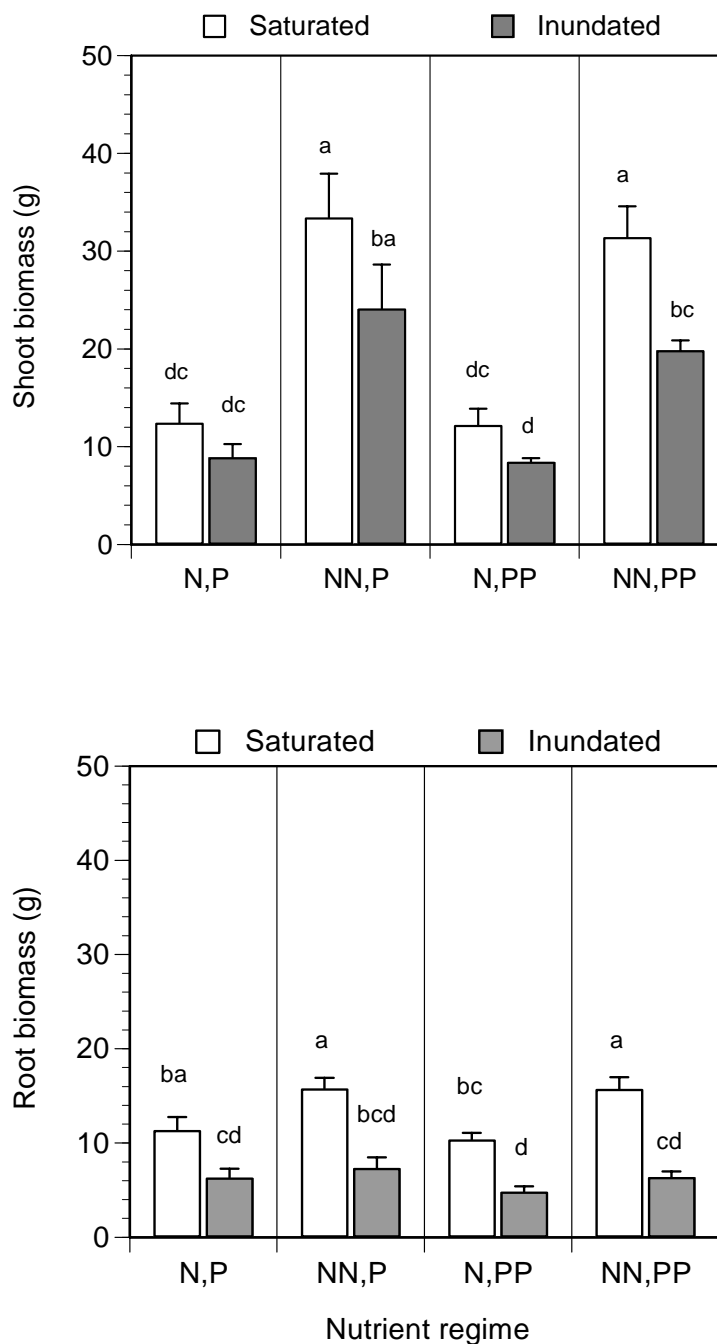


Figure 2.3. The effect of manipulated nutrient availability and hydrology on Panicum hemitomon shoot (top panel) and root biomass (g) (bottom panel) for the phase – II study, measured at harvest after four months of growth. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,P = high nitrogen and low phosphorous; N,PP = low nitrogen and high phosphorous; NN,PP = high nitrogen and high phosphorous. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for shoot ($F_{7,32} = 16.25$, $p < 0.0001$) and root biomass ($F_{7,32} = 18.27$, $p < 0.0001$).

Rhizome biomass for the phase – II study (Figure 2.4, top panel; Appendix, Table 3) followed suit with shoot and root biomass with respect to dry biomass. Significantly greater rhizome biomass was associated with nitrogen enrichment ($F_{3,32} = 8.40$, $p = 0.0003$), and in saturated, as opposed to inundated, hydrologic conditions ($F_{1,32} = 80.63$, $p < 0.0001$). Together, saturation (0 cm flooding) and nitrogen enrichment ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$) resulted in more than twice as much rhizome biomass as compared to inundation (15 cm flooding) and non-enriched ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$) nitrogen conditions. Although not statistically significant, the greater rhizome biomass observed in saturated hydrologic conditions and phosphorous enrichment, but non-enriched nitrogen conditions, is of interest because phosphorous enrichment is generally associated with greater root growth, but few studies have associated greater rhizome growth with phosphorous enrichment. The nutrient by hydrology interaction was not significant.

Rhizome length in the phase – II study (Figure 2.4, bottom panel; Appendix, Table 4) mirrored rhizome biomass in that it was significantly greater under nitrogen enrichment ($F_{3,32} = 4.04$, $p = 0.0153$), and in saturated, as compared to inundated, hydrologic conditions ($F_{1,32} = 80.63$, $p < 0.0001$). Although greater total rhizome length was associated with saturated hydrologic conditions (0 cm flooding), nitrogen enrichment enhanced rhizome length under both saturation and inundation. Interestingly, saturated conditions with enriched phosphorous, but non-enriched nitrogen availability, increased rhizome length more than it did overall rhizome biomass or root biomass.

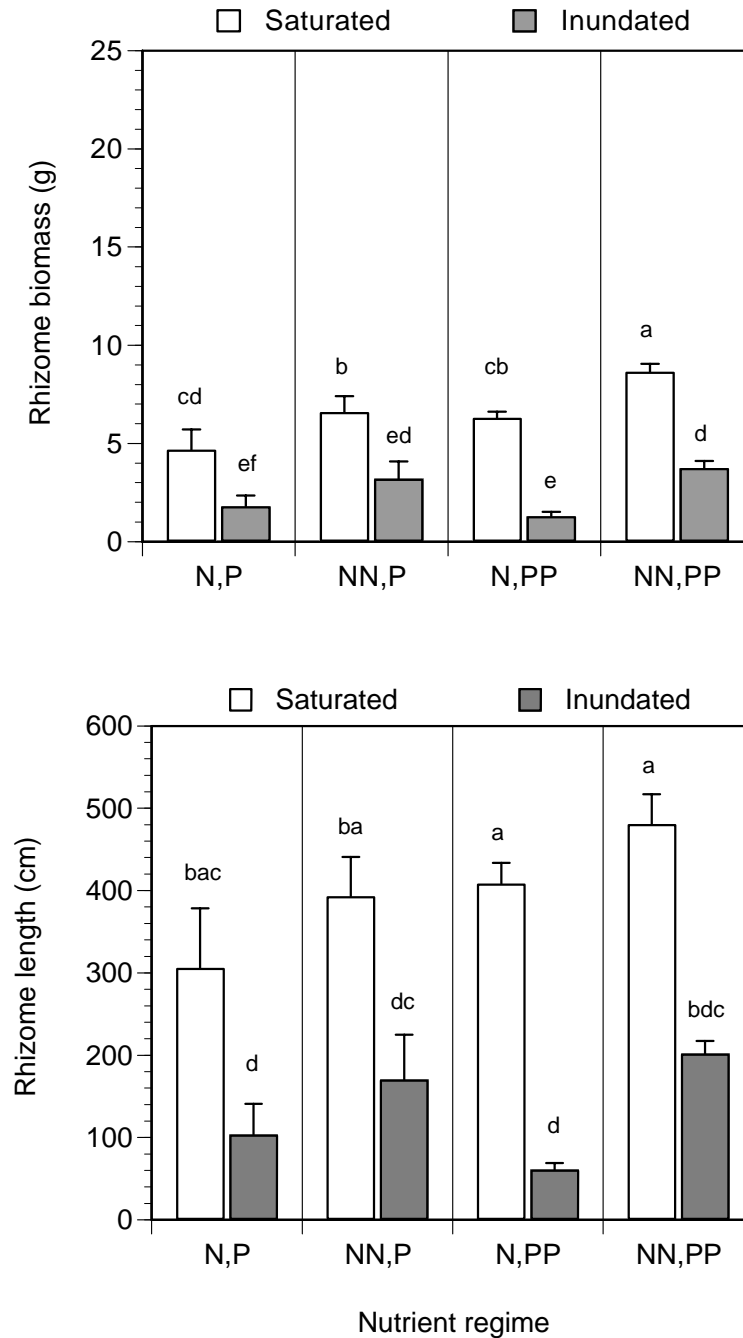


Figure 2.4. The effect of manipulated nutrient availability and hydrology on Panicum hemitomon rhizome biomass (g) (top panel) and rhizome length (cm) (bottom panel) for the phase – II study, measured at harvest after four months of growth. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,P = high nitrogen and low phosphorous; N,PP = low nitrogen and high phosphorous; NN,PP = high nitrogen and high phosphorous. Values are means \pm SE (n = 5). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for rhizome biomass ($F_{7,32} = 15.72$, $p < 0.0001$) and rhizome length ($F_{7,32} = 13.49$, $p < 0.0001$).

As anticipated, based on results of independent measures of shoot, rhizome, and root biomass, Panicum hemitomon total biomass in the phase – II study (Figure 2.5 top and bottom panels; Appendix, Table 4) was significantly greater under nitrogen enrichment ($F_{3,32} = 29.09$, $p < 0.0001$), and in saturated, as compared to inundated, hydrologic conditions ($F_{1,32} = 60.19$, $p < 0.0001$). When saturated treatments were assessed independently (Appendix, Table 4), it became clear that total biomass associated with nitrogen enrichment ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$) was double that observed under non-enriched conditions ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$). This increase was largely due to increased shoot production, and to a lesser extent, increased rhizome and root production. Similar effects were observed for inundated treatments, with nitrogen enrichment greatly enhancing Panicum hemitomon total production, although biomass totals were less than those observed in saturated treatments. Phosphorous enrichment did not augment Panicum hemitomon production in either hydrologic regime. Moreover, the nutrient by hydrology interaction was not significant.

Taking into account total biomass, and all partitions of Panicum hemitomon biomass (shoot, rhizome, and root biomass), it is clear that saturated hydrologic conditions were more conducive for growth than were inundated conditions. With respect to nutrient regime, it is obvious that nitrogen enrichment enhanced all partitions of Panicum hemitomon biomass (Image 2.2).

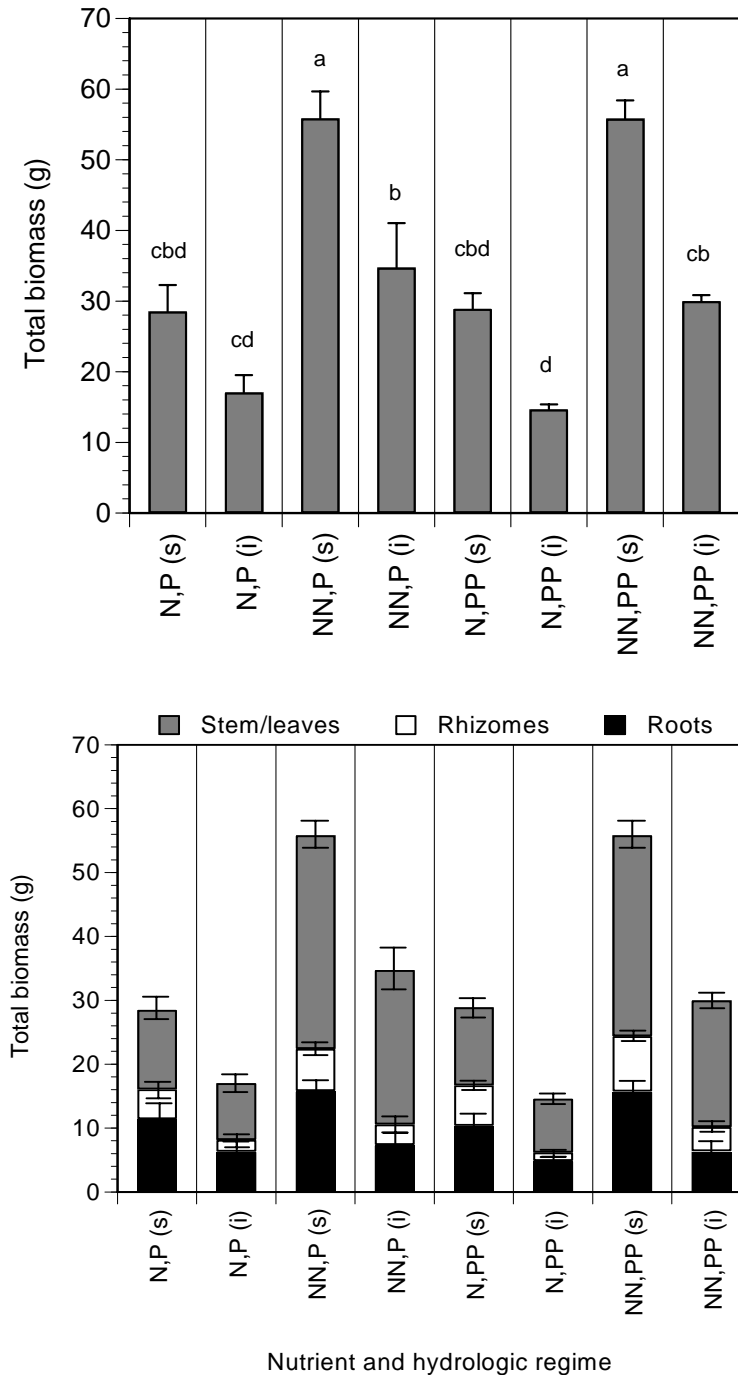


Figure 2.5. The effect of manipulated nutrient availability and hydrology on Panicum hemitomon total biomass (g) (top panel) and total biomass separated into specific components (g) (bottom panel) for the phase – II study, measured at harvest after four months of growth. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,P = high nitrogen and low phosphorous; N,PP = low nitrogen and high phosphorous; NN,PP = high nitrogen and high phosphorous; s = saturated; i = inundated. Values are means \pm SE (n = 5). Letters over bars represent significantly different means (Tukey's pairwise comparisons, α = 0.05; $F_{7,32}$ = 21.89, p < 0.0001).

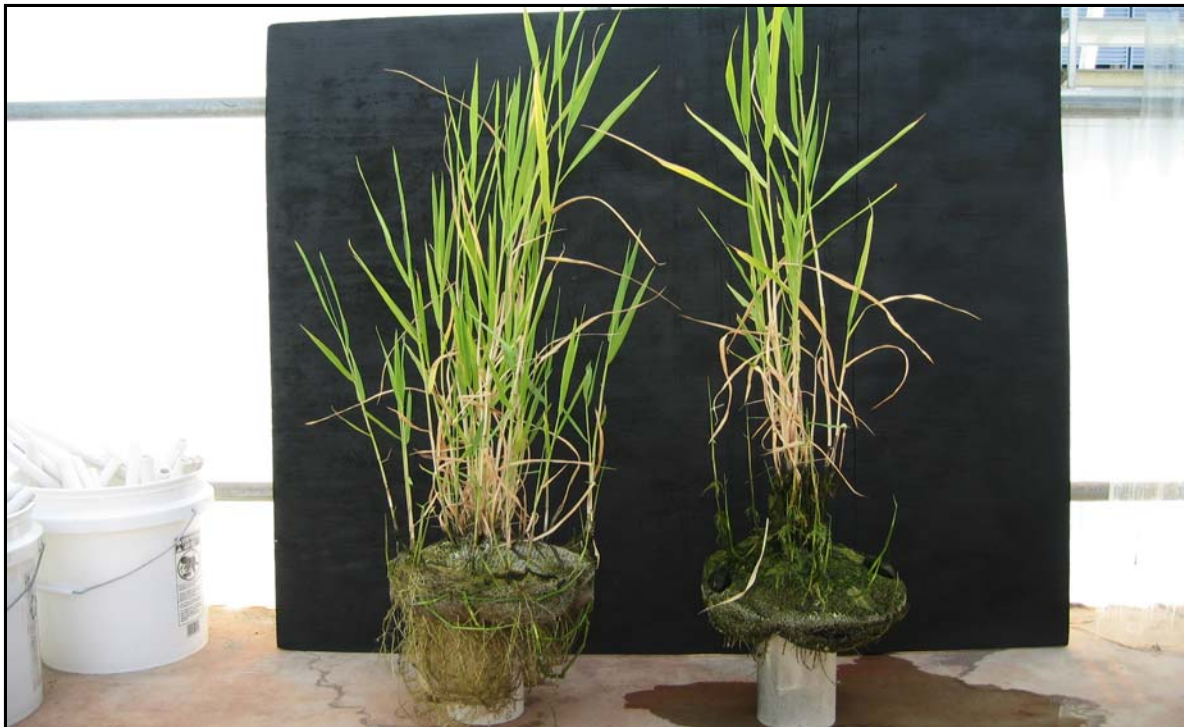


Image 2.2. *Panicum hemitomon* growth for the phase – II study, under non-enriched nitrogen and phosphorous availability, left plant grown in inundated and right in saturated conditions (top image); *Panicum hemitomon* growth under enriched nitrogen and phosphorous availability, left plant grown in saturated and right in inundated conditions (bottom image).

When partitions of total biomass were viewed on a proportional basis (Figure 2.6; Appendix, Table 5), statistically significant treatment effects were observed for shoot, rhizome, and root contributions. The proportion of total biomass represented by shoot biomass varied significantly according to both the main effects of nutrient ($F_{7,32} = 17.35$, $p < 0.0001$) and hydrologic regime ($F_{1,32} = 33.17$, $p < 0.0001$), with the largest proportions observed under nitrogen enrichment ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$), and in inundated hydrologic conditions (15 cm flooding). The nutrient by hydrology interaction was not significant. In contrast, the proportion represented by rhizome biomass was not as affected by nutrient regime, although still significant ($F_{7,32} = 3.07$, $p < 0.0418$), whereas the effect of hydrologic regime was highly significant ($F_{1,32} = 23.30$, $p < 0.0001$). Rhizome contribution was greatest in saturated treatments (0 cm flooding). The nutrient by hydrology interaction was not significant. Similarly, root contribution exhibited significant nutrient ($F_{7,32} = 18.91$, $p < 0.0001$) and hydrologic effects ($F_{1,32} = 10.31$, $p < 0.0001$), and compared to shoot and rhizome contribution, was most strongly influenced by nutrient regime, with non-enriched nitrogen treatments ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$) resulting in the greatest root contributions. The effect of phosphorous enrichment ($10 \text{ g P m}^{-2} \text{ yr}^{-1}$) on proportional partitions of biomass, regardless of hydrologic regime, was much less than that observed for nitrogen enrichment.

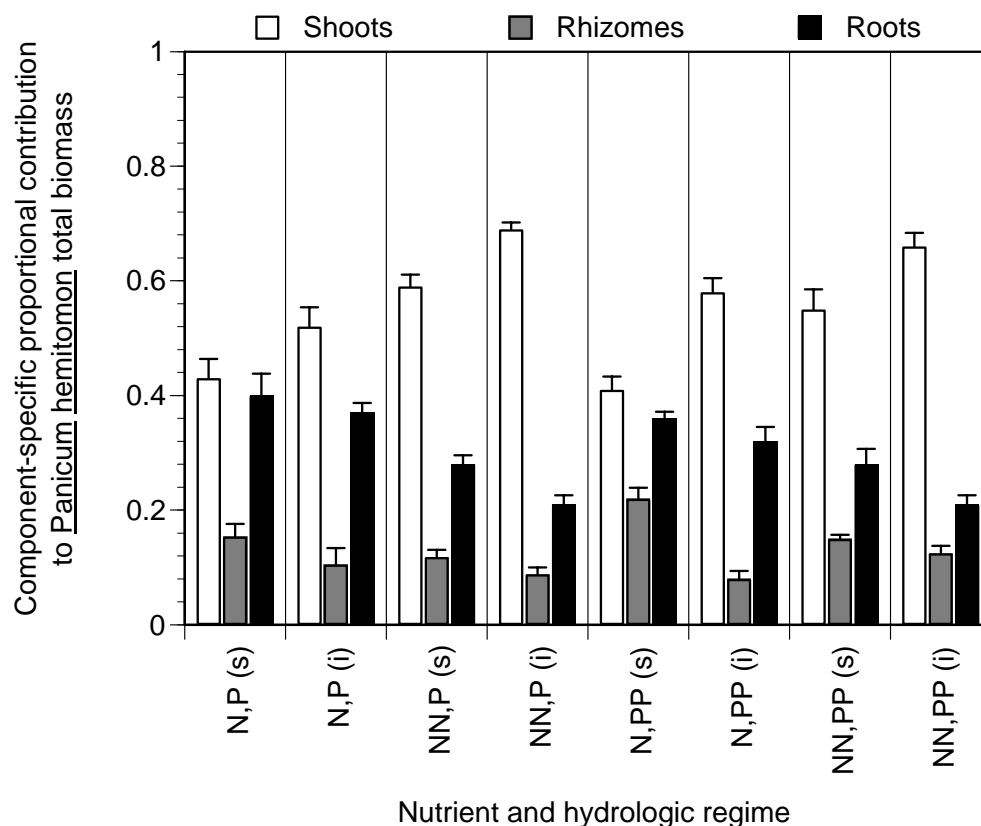


Figure 2.6. The effect of manipulated nutrient availability and hydrology on component-specific proportional contributions to Panicum hemitomon total biomass for the phase – II study, measured at harvest after four months of growth. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,P = high nitrogen and low phosphorous; N,PP = low nitrogen and high phosphorous; NN,PP = high nitrogen and high phosphorous; s = saturated; i = inundated. Values are means \pm SE (n = 5).

Panicum hemitomom root:shoot ratios in the phase – II study (Figure 2.7; Appendix, Table 6) were significantly greater under non-enriched nitrogen availability ($F_{3,32} = 12.31$, $p < 0.0001$), and in saturated, as compared to inundated, hydrologic conditions ($F_{1,32} = 13.41$, $p = 0.0009$). Root:shoot ratios were significantly less (i.e., greater shoot biomass relative to root biomass) for both saturated and inundated treatments when in conjunction with nitrogen enrichment. The effects of phosphorous were negligible, and the nutrient by hydrology interaction was not significant.

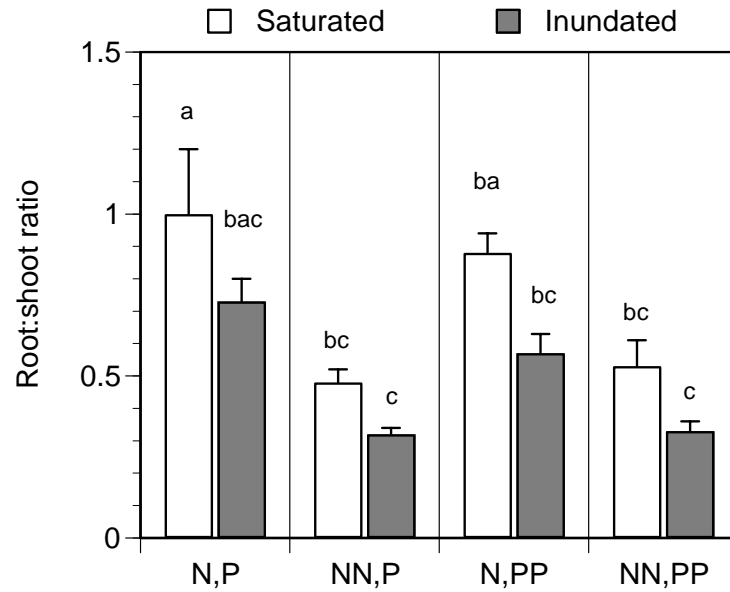


Figure 2.7. The effect of manipulated nutrient availability and hydrology on Panicum hemitomon root:shoot ratio for the phase – II study, measured at harvest after four months of growth using entire root systems. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,P = high nitrogen and low phosphorous; N,PP = low nitrogen and high phosphorous; NN,PP = high nitrogen and high phosphorous. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for root:shoot ratio ($F_{7,32} = 7.30$, $p < 0.0001$).

Root morphological data

Panicum hemitomon root specific gravity was measured in both the phase – I and phase – II studies. For the phase – I study (Figure 2.8, top panel), root specific gravity did not vary with either the main effect of nutrient or hydrologic regime. The nutrient by hydrology interaction was not significant either.

Similar results were observed for the phase – II study (Figure 2.8, bottom panel). While root specific gravity was somewhat greater in inundated hydrologic conditions, and to a lesser extent under nitrogen and phosphorous enrichment, neither the main effect of nutrient nor hydrologic regime was significant. The nutrient by hydrology interaction was not significant.

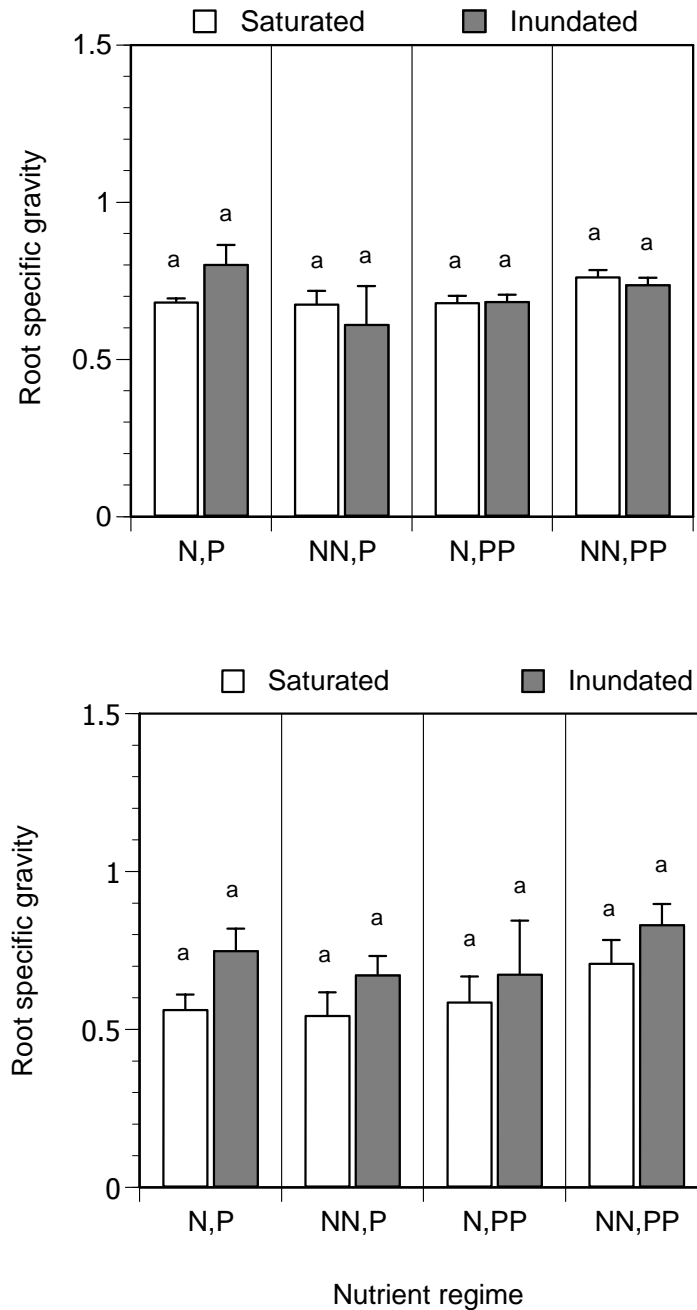


Figure 2.8. The effect of manipulated nutrient availability and hydrology on Panicum hemitomon root specific gravity for phase – I (top panel) and phase – II (bottom panel), measured on live root tissue several months after initiation in both phases. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,P = high nitrogen and low phosphorous; N,PP = low nitrogen and high phosphorous; NN,PP = high nitrogen and high phosphorous. Values are means \pm SE (n = 5). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for phase – I ($F_{7,32} = 1.13$, $p = 0.3714$) and phase – II ($F_{7,32} = 1.32$, $p = 0.2729$).

Root volume for the phase – II study (Figure 2.9; Appendix, Table 6) was significantly greater under nitrogen enrichment ($F_{3,32} = 4.09$, $p = 0.0145$), and in saturated, as compared to inundated, hydrologic conditions ($F_{1,32} = 51.71$, $p < 0.0001$). The nutrient by hydrology interaction was also significant ($F_{3,32} = 4.14$, $p = 0.0138$), highlighted by an unexpected decrease in root volume under the combined effects of inundation and nitrogen and phosphorous enrichment. To further elucidate this relationship, saturated and inundated treatments were assessed independently (Appendix, Table 6). With saturation, a significant trend for greater root volume was observed under nitrogen enrichment ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$), and to a lesser extent, under phosphorous enrichment ($10 \text{ g P m}^{-2} \text{ yr}^{-1}$).

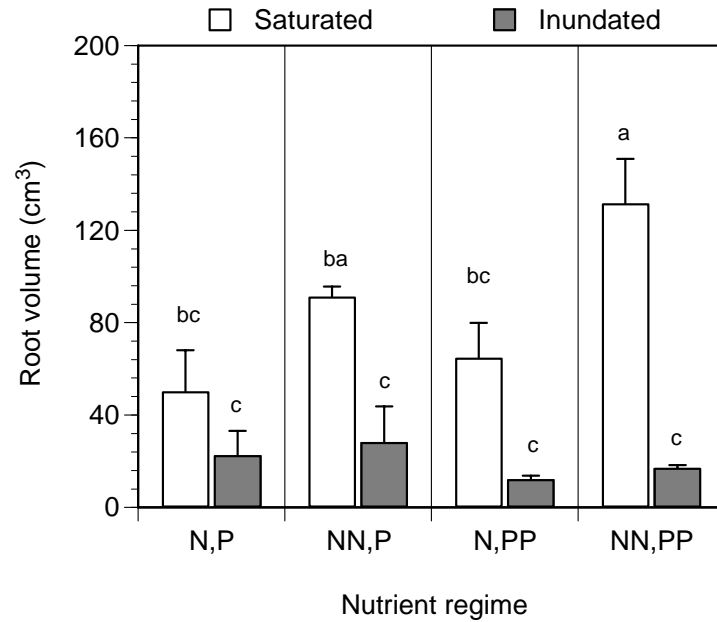


Figure 2.9. The effect of manipulated nutrient availability and hydrology on Panicum hemitomon total root volume (cm³) for the phase – II study, measured at harvest after four months of growth using entire root systems. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,P = high nitrogen and low phosphorous; N,PP = low nitrogen and high phosphorous; NN,PP = high nitrogen and high phosphorous. Values are means \pm SE (n = 5). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for root:shoot ratio ($F_{7,32} = 7.30$, $p < 0.0001$) and root volume ($F_{7,32} = 10.92$, $p < 0.0001$).

Panicum hemitomom mean root diameter for the phase – II study (Table 2.2; Appendix, Table 7) did not respond significantly to nutrient enrichment, although it was greater in inundated, as compared to saturated, hydrologic conditions ($F_{1,152} = 6.82$, $p = 0.0099$). A trend for greater mean root diameter was observed in inundated and phosphorous-enriched conditions, with smaller mean root diameters observed for saturated and non-enriched nitrogen and phosphorous treatments. The nutrient by hydrology interaction was not significant.

Panicum hemitomom mean root length for the phase – II study (Table 2.2; Appendix, Table 7) showed no response to nutrient enrichment, although sub-sampled roots were longer under saturated, as compared to inundated, hydrologic conditions ($F_{1,152} = 115.81$, $p < 0.0001$). Greater mean root length was associated with saturated hydrologic conditions regardless of nutrient regime, and to a lesser extent, with non-enriched ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$) nitrogen conditions. The nutrient by hydrology interaction was not significant.

Similarly, Panicum hemitomom mean root volume for the phase – II study (Table 2.2; Appendix, Table 7) did not respond to nutrient enrichment, but it was significantly greater in saturated, as compared to inundated, hydrologic conditions ($F_{1,152} = 155.38$, $p = < 0.0001$). Greater mean root volume was associated with saturated hydrologic conditions regardless of nutrient regime, and to a lesser extent, with phosphorous enrichment ($10 \text{ g P m}^{-2} \text{ yr}^{-1}$). The nutrient by hydrology interaction was not significant.

As with other root morphological attributes, the mean number of root tips observed for the phase – II study (Table 2.2; Appendix, Table 7) was not significantly affected by nutrient enrichment, but was significantly greater in saturated, as compared to inundated, hydrologic conditions ($F_{1,152} = 129.26$, $p < 0.0001$). Saturated hydrologic conditions, and to a lesser extent, non-enriched nitrogen availability, appeared to augment the number of root tips. The nutrient by hydrology interaction was not significant.

Table 2.2. The effect of manipulated nutrient availability and hydrology on *Panicum hemitomon* individual mean root diameter (mm), length (cm), volume (cm³), and number of root tips for the phase – II study. All measurements were performed on live root tissue sampled immediately prior to experimental harvest. Values are means \pm SE (n = 20).

Treatment	Diameter (mm)	Length (cm)
N,P (saturated)	0.43 \pm 0.024 ^b	303.25 \pm 47.23 ^a
N,P (inundated)	0.50 \pm 0.044 ^{ba}	119.45 \pm 37.96 ^b
NN,P (saturated)	0.46 \pm 0.014 ^{ba}	240.99 \pm 21.14 ^a
NN,P (inundated)	0.45 \pm 0.019 ^{ba}	71.22 \pm 12.88 ^b
N,PP (saturated)	0.44 \pm 0.019 ^{ba}	329.75 \pm 31.89 ^a
N,PP (inundated)	0.53 \pm 0.022 ^a	43.62 \pm 6.17 ^b
NN,PP (saturated)	0.46 \pm 0.008 ^{ba}	250.20 \pm 24.47 ^a
NN,PP (inundated)	0.49 \pm 0.020 ^{ba}	58.57 \pm 8.26 ^b
<i>F</i> – value (df 7,152)	2.00 [*]	18.20 ^{**}

Treatment	Volume (cm ³)	Tips (#)
N,P (saturated)	0.37 \pm 0.060 ^a	1169.70 \pm 182.34 ^a
N,P (inundated)	0.17 \pm 0.044 ^b	352.05 \pm 87.82 ^b
NN,P (saturated)	0.43 \pm 0.038 ^a	872.60 \pm 70.05 ^a
NN,P (inundated)	0.09 \pm 0.013 ^b	290.25 \pm 61.48 ^b
N,PP (saturated)	0.46 \pm 0.032 ^a	1250.45 \pm 138.76 ^a
N,PP (inundated)	0.08 \pm 0.005 ^b	197.15 \pm 23.49 ^b
NN,PP (saturated)	0.42 \pm 0.037 ^a	950.70 \pm 96.60 ^a
NN,PP (inundated)	0.09 \pm 0.010 ^b	201.55 \pm 23.41 ^b
<i>F</i> – value (df 7,152)	23.24 ^{**}	20.08 ^{**}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference ($p < 0.01$); ^{*} significant difference ($p < 0.05$); ^{NS} non-significant difference ($p > 0.05$).

Regardless of nutrient or hydrologic regime, at least 70 percent of total root system length fell into the smallest root diameter class (0.0 – 0.49 mm) (Figure 2.10, top panel; Appendix Table 8). For illustrative purposes, Figure 2.10 only shows the lowest and highest nitrogen and phosphorous loading rates for both saturated and inundated treatments. However, all other treatments (Appendix, Table 8) exhibited similar within-group patterns. Although much less influential, the 1.0 – 1.49 mm diameter class was the second most represented for all treatment combinations, but unlike the 0.0 – 0.49 mm class, a slightly larger proportion of inundated treatments were associated with this root diameter class. Root systems of inundated treatment groups had slightly larger proportions of root length in larger diameter classes, and less in the smallest diameter class, than did root systems experiencing saturated hydrologic conditions.

Total root volume for the phase - II study (Figure 2.10, bottom panel; Appendix, Table 9) was more evenly distributed across diameter classes than was root length, with the 1.0 – 1.49 mm diameter class contributing the most to total volume. Again, for illustrative purposes, Figure 2.10 shows only the lowest and highest nitrogen and phosphorous loading rates for both saturated and inundated treatments. However, all other treatments (Appendix, Table 9) exhibited similar patterns. Overall, there was considerable variation among treatments within each root diameter class, with no particularly noteworthy patterns or trends. The one exception is that saturated treatments were better represented in 1.5 – 1.99 mm root diameter class, whereas inundated treatments were better represented in the slightly smaller, 1.0 – 1.49 mm root diameter class.

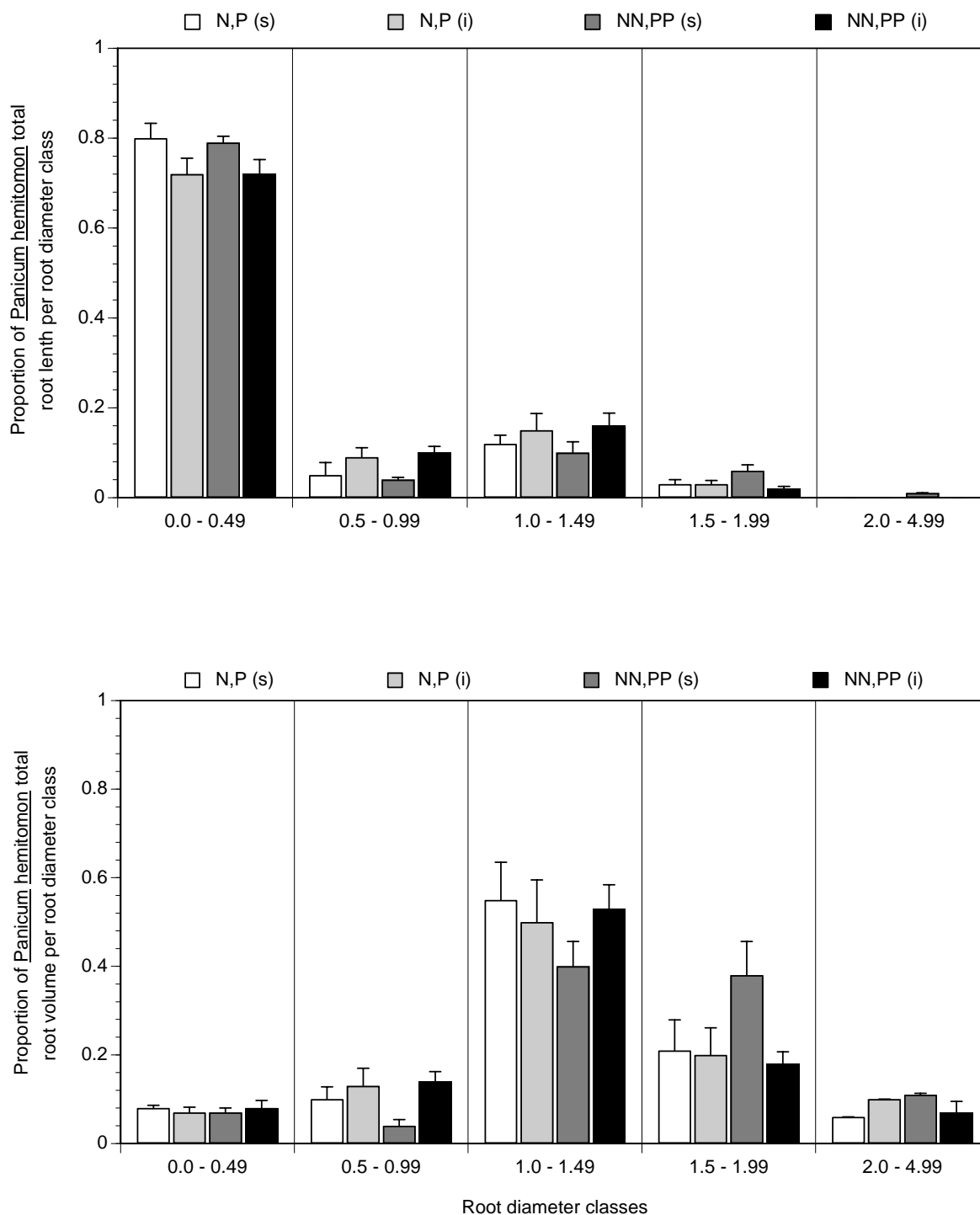


Figure 2.10. The proportion of *Panicum hemitomon* total root length (cm) (top panel) and total root volume (cm³) (bottom panel) per root diameter class (mm) for the phase – II study, measured at harvest after four months of growth using entire root systems. Treatment codes are as follows: N,P = low nitrogen and low phosphorous; NN,PP = high nitrogen and high phosphorous; s = saturated; I= inundated. Values are means \pm SE (n = 5).

Discussion

This research demonstrated that nutrient and hydrologic regime can be manipulated in ways that result in Panicum hemitomom growth and patterns of biomass allocation that benefit floating marsh restoration. Having said this, the findings reported here do not attempt to independently make recommendations for such purposes at this point, rather they should be interpreted collectively with other results reported herein, and with important findings from previous studies, so that key results and differences in respective experimental designs can be accounted for. It is important to recognize, regarding the context of this research, that for hydrologic regime, some detailed and applicable information exists, but for nitrogen and phosphorous loading rates, detailed scientific information is largely unavailable.

An increase in the nitrogen loading rate from 25 to 50 g N m⁻² yr⁻¹ resulted in significant increases in both above- and belowground production. Shoot biomass was significantly greater under nitrogen enrichment (50 g N m⁻² yr⁻¹), whereas the influence of phosphorous was less pronounced. This pattern follows the paradigm that plant phosphorous requirements tend to be lower than nitrogen requirements, and that phosphorous enrichment, unlike nitrogen enrichment, is not as directly reflected in tangible plant growth (Chapin 1980). The positive response of shoot production to nitrogen enrichment was expected because nitrogen enrichment is known to increase shoot production in other grass species (Chapin et al. 1986; Di Tomasso and Aarsen 1989). The influence of nutrient regime on belowground production was less predictable because rhizome and root responses, including morphological attributes of entire root systems, vary widely within and among plant taxa due to soil textural heterogeneity and the spatial and temporal variability of nutrient pools (Badalucco and Kuikman 2001; de Kroon and Visser 2003).

Plants in general respond to nutrient limitation via compensatory changes such as increased root absorption capacity for limiting nutrients, increased root:shoot ratio, or decreased photosynthetic output (Chapin et al. 1986). In this study, I observed changes that support these general patterns. For example, in the phase – II study, net CO₂ assimilation rates were highest under nitrogen enrichment (50 g N m⁻² yr⁻¹) and saturated (0 cm flooding) conditions, as compared to non-enriched (25 g N m⁻² yr⁻¹) and inundated (15 cm flooding) conditions. Also in agreement with Chapin et al. (1986), I observed greater root:shoot ratios under non-enriched nutrient conditions. The responses I observed in inundated and non-enriched treatments may have been exacerbated by a positive feedback between inadequate nutrient absorption and insufficient root biomass. In particular, the limited root production observed under inundated conditions may have initially limited nutrient absorption, but over time, may have lead to decreases in CO₂ assimilation resulting from insufficient nitrogen availability for photosynthetic processes, an effect reported elsewhere under flooding and low nutrient availability (Sharkey et al. 2004).

Photosynthetic nitrogen-use efficiency (PNUE), the photosynthetic rate per unit leaf nitrogen, provides a reliable measure of how efficiently available nitrogen is being utilized for carbon fixation (Lambers et al. 1998). It is generally understood that as nitrogen availability and uptake increase, plant nitrogen use-efficiency decreases (Crawley 2005). In a controlled-setting study employing three grass and one sedge species, Pons et al. (1994) concluded that PNUE was greater for all species under low nitrogen availability. They also noted significant differences in species-specific growth rates under high nitrogen availability. The species that exhibited the smallest increase in leaf nitrogen (*Dactylis glomerata* L.), was also associated with the smallest reduction in PNUE, whereas other species tended to accumulate nitrogen in their leaves without proportional increases in photosynthetic rate. In my research, significant

differences in Panicum hemitomom PNUE were not observed for either phase. Considering the difference in nitrogen availability between non-enriched and enriched treatments (i.e., double the rate), no significant differences in PNUE may indicate that Panicum hemitomom is efficiently utilizing increases in available nitrogen for greater assimilation and growth, rather than for luxury compensation and storage.

Root systems of monocots, including grasses like Panicum hemitomom, are generally extremely dense and fibrous, often lacking a noticeable tap root (Di Tomasso and Aarsen 1989; de Kroon and Visser 2003). Such root systems are also characterized by many small-diameter (≥ 5 mm) lateral roots (Weaver 1968; de Kroon and Visser 2003). Panicum hemitomom grown under nitrogen enrichment exhibited these qualities. Additionally, vigorously growing plants concentrated a substantial amount of root biomass, particularly fine root biomass, in the upper portion of the vegetated mat, a trait common among many grasses, although more typically in reference to near-surface soil layers of terrestrial settings (Kutschera and Lichtenegger 1992). Whereas the surface layers were dominated by fine root material, larger diameter, coarse root material dominated at depth within the vegetated mat, and in the water column directly beneath the mat. A substantial amount of root material was also associated with laterally-growing rhizomes, a characteristic that Kutschera and Lichtenegger (1992) and Hook et al. (1994) associate with clonal grasses.

Rhizome growth was a key variable assessed in this research not only because of its association with Panicum hemitomom lateral spreading potential, but because greater rhizome biomass should imply greater mat structural integrity and buoyancy as a result of gas trapping and air storage in rhizome inter-nodal spaces, a characteristic exhibited by some flood-tolerant species (Sorrell et al. 1997). Whereas inundation was detrimental to rhizome growth across all nutrient treatments, rhizome growth responded favorably to nitrogen enrichment, although

differences in biomass and length under non-enriched conditions were not as pronounced as with shoot or root biomass. Moreover, and to a much greater extent than for other parts, rhizome growth was influenced by phosphorous enrichment, an effect that may provide support for the greater buoyancy of floating marsh sods observed by Fisher (2003) under phosphorous enrichment.

The relative partitioning of biomass into either above- or belowground components was important here because root mat structural integrity and buoyancy may decrease if enhanced aboveground production occurs at the expense of belowground production. In this study Panicum hemitomon responded to nitrogen enrichment with increased biomass, and the increased net CO₂ assimilation rates discussed earlier, yet with decreased root:shoot ratios. Although root:shoot ratios decreased under nitrogen and phosphorous enrichment, it is doubtful that such small changes are ecologically significant, or below the threshold that could impair the buoyancy and stability of created thick-mat floating marsh. Important directions for future research will be investigating the effects of excessive nitrogen loading on floating marsh mat structural integrity and buoyancy, plant community composition, and long-term marsh stability.

When wetlands become flooded, oxygen diffusion and availability decrease markedly, resulting in the development of reduced soil conditions, which together with other biologically and chemically-mediated changes, increase the level of physiological stress in the rooting environment (Gambrell et al. 1991; Cronk and Fennessy 2001). Flooding is therefore widely regarded as a plant stressor for nearly all terrestrial species, and for many wetland-adapted species (Jackson 1990; Blom et al. 1996; Jackson and Armstrong 1999). In this study, I expected root specific gravity to decrease under inundation because tissue porosity in wetland-adapted plants, and in some non-wetland species, is known to increase under oxygen limitation due to enhanced aerenchyma formation (Evans 1994; Cronk and Fennessy 2001). Despite

slightly greater mean root diameters under inundated conditions, no significant differences in root specific gravity were observed. I attribute this result to several factors including water-logging in non-vigorous and porous roots, and to a lesser degree, the possible use of senescent roots for some analyses. Some of the roots sampled from plants grown under inundated conditions appeared waterlogged during harvest, and later in lab analyses. It is also possible that aerenchyma development may have occurred initially in roots exposed to inundated conditions, resulting in an increase in root diameter. However, with prolonged flooding stress and a decrease in vigor, some of these roots may have lost structural integrity by the end of the experiment. Another possible explanation is that stem-borne adventitious roots superceded other, less vigorous roots growing at depth with respect to key physiological processes, resulting in a decrease in vigor of those roots growing under more stressful oxygen-limited conditions. Aside from flooding stress, nitrogen and phosphorous limitation (Drew et al. 1989), and to a lesser degree sulfate stress (Bouranis et al. 2003), are known to enhance aerenchyma development. This may have contributed to the lower specific gravity root tissue observed under dual non-enriched nitrogen and phosphorous conditions. As mentioned earlier, Fisher (2003) assessed buoyancy in Panicum hemitomon-dominated floating marsh sods and observed a tendency for reduced sod buoyancy under nitrogen enrichment, with the effects of phosphorous being possibly beneficial for buoyancy. Whether such effects influenced the results reported here is not known because the buoyancy of small-diameter vegetated mats would have been difficult to accurately assess given the way in which they were constructed and maintained in their respective experimental vessels, and considering the time frame allowed for growth and development before harvest. Nevertheless, the increase in rhizome biomass observed under phosphorous enrichment may provide support for greater sod buoyancy as described earlier.

It has been demonstrated previously that many Panicum hemitomon growth-related metrics, notably stem height and biomass, respond positively to hydrologic inundation (Hester et al. 1998; Fisher 2003; Kirkman and Sharitz 2003; Willis and Hester 2004; Spalding and Hester 2007). The research described here mainly supports, yet sometimes contradicts, these earlier findings. Kirkman and Sharitz (1993) observed elongated stems under inundated conditions, along with a greater number of stems and greater aboveground biomass. Willis and Hester (2004), and Fisher (2003), both subjected Panicum hemitomon to moderate levels of flooding (10 and 15 cm respectively), and like Kirkman and Sharitz (1993), they too observed elongated stems. However, these authors observed different biomass allocation patterns. Willis and Hester (2004) reported increased above- and belowground production under moderately flooded conditions, whereas Kirkman and Sharitz (1993) observed greater aboveground production, but decreased belowground production. In a mesocosm study, Spalding and Hester (2007) reported significant increases in Panicum hemitomon above- and belowground biomass under moderate (+5 or +20 cm) freshwater flooding compared to mesic (-10 cm water table) conditions. Clearly, Panicum hemitomon response to moderate flooding varies, and may be influenced by soil type as well as by ecotypic variation (Hester et al. 1998).

Elucidating the effects of manipulated nutrient availability and hydrology on Panicum hemitomon belowground production was an important objective of this research because robust root and rhizome growth are imperative for creating a structurally-sound and buoyant root mat. Conditions that enhance rhizome and root growth, while promoting low specific gravity root tissue, are most desirable for floating marsh restoration. Tradeoffs may exist, however, between allocation to belowground biomass and construction of lower specific gravity roots. Providing conditions that equally benefit above- and belowground production should be promoted not only to enhance mat structural integrity and buoyancy, but because robust shoot

production is necessary for plant vigor, and for many of the habitat-providing services contributed by floating marsh.

The results of this research suggest that saturated hydrologic conditions (0 cm flooding) are more accommodating for robust Panicum hemitomon growth than inundated (15 cm flooding) hydrologic conditions. They also suggest that nitrogen enrichment at the peak range of mean levels observed at the Caernarvon diversion ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$) benefits both above- and belowground Panicum hemitomon production. This is not to say that the vigorous Panicum hemitomon growth required for floating marsh restoration cannot be achieved under non-enriched conditions, because even the non-enriched conditions employed here exceed normal background levels (i.e., approximately $7 \text{ g N m}^{-2} \text{ yr}^{-1}$) for floating, and other freshwater, marshes in Louisiana (Delaune 1986; Bowden 1987; Sasser 1994). From an applied restoration perspective, it may be advantageous to initially fertilize created mats with a higher-than-normal loading rate to jump-start young plants, followed by periodic non-enriched applications, or no application at all. I feel that such benefits are achievable under the non-enriched conditions employed here. Using non-enriched conditions would also tend to minimize potentially undesirable long-term shifts in Panicum hemitomon allocation patterns, but equally as important, would decrease the potential for undesirable shifts in species composition in adjacent naturally-formed marshes that may be susceptible to such nutrient effects. In addition to meeting a priori objectives, this research provides valuable insight into how naturally-formed Panicum hemitomon-dominated floating marshes may respond to nutrient amendment. To further elucidate such effects, additional manipulative studies in both field and controlled settings are warranted.

Chapter 3

The Effect of Substrate Material and Mat or Containment Material on Growth Response and Patterns of Biomass Allocation by Panicum hemitomon

Introduction

Primary objectives

The primary objectives of these experiments were to elucidate Panicum hemitomon growth response and patterns of biomass allocation as influenced by substrate and mat or containment materials. These data are particularly crucial because under conditions associated with floating marsh restoration, not only must all substrate material be supplied, and consequently suitable for plant growth, but mat materials must be effective at containing the substrate, which, as observed with fine-textured peat, may be challenging based on particle size and fluidity upon submergence. Moreover, all materials must be of low specific gravity to promote the buoyancy of created mats. In field settings where floating marsh restoration has been proposed (i.e., areas where it has been lost), water depths tend to be too great and/or substrates too unconsolidated for the establishment of emergent vegetation. Hence the rationale behind deploying floating mats into such areas. Because of the need to utilize materials that promote vigorous plant growth, and the fact that no previous study has assessed Panicum hemitomon growth response under such a scenario, it was important to quantitatively evaluate a suite of substrate and mat or containment materials to identify those most suitable for restoration purposes.

Background

In addition to being crucial for lateral spread and the establishment of daughter ramets, anchorage, and water acquisition and mineral nutrient uptake, robust Panicum hemitomon

rhizome and root production, as discussed earlier, is required for floating mat structural integrity and buoyancy. It was therefore important to elucidate Panicum hemitomom relative growth response, particularly rhizome and root production, as influenced by environmental conditions other than nutrient and hydrologic regime, that were considered important given the restoration context of this research. To achieve this, I assessed Panicum hemitomom growth response in conjunction with a suite of substrate and mat or containment materials.

Important in this assessment is that previous studies assessing Panicum hemitomom growth under semi-controlled experimental settings have utilized different planting mediums or substrate materials, none of which would be suitable for floating marsh restoration purposes. Kirkman and Sharitz (1993) used sand that was largely void of organic matter, whereas Pezeshki et al. (2000) used two commercially-available potting mixes, that in addition to an unspecified mineral content, also contained nutrient supplements and ailing and wetting agents. More recently, Willis and Hester (2004) grew Panicum hemitomom in moderately organic mediums (36% and 63% organic matter by weight), whereas Spalding and Hester (2007) used a commercially-blended soil containing 34% organic matter. As detailed in the Materials and Methods section that follows, the materials I used in this study differed from the before mentioned in that they all were plant-derived materials that lacked a mineral component because of concerns over mat buoyancy. As a result, growth responses as reported in other studies were useful for comparative purposes, but were not adoptable for floating marsh restoration.

The heterogeneity exhibited by most naturally-formed soils in terms of texture and mineral content affects all aspects of plant growth, but particularly root growth (Snaydon 1962; Jackson and Caldwell 1993; Jackson et al. 1996 and 1997). Root system structure and morphology, total root production, and the proliferation of lateral roots are all directly affected

by soil or substrate characteristics (de Kroon and Visser 2003). Mechanically impeded roots not only tend to be shorter than roots grown in loose or un-impeded mediums, but root diameter may increase by as much as a factor of two (Materechera et al. 1999). Goss (1977) grew Hordeum vulgare in impeded and unimpeded mediums and came to the conclusion that despite the fact that there were twice as many lateral roots per unit length of seminal root in the impeded medium, the total number of laterals remained unchanged because seminal roots were shorter. In other words, shorter roots resulted in a two-fold increase in the total number of lateral roots per unit length of seminal root. In mediums that are both compacted and anaerobic, root growth may decrease as a result of nutrient limitation (Dejong-Hughes et al. 2001) and/or hypoxic conditions (Gambrell et al. 1991; de Kroon and Visser 2003). The planting mediums or substrate materials assessed in this study were not only all plant-derived, but were all permanently immersed in water once experimental treatments were applied. Therefore, substrate compaction and impedance were not of significant concern. What was of concern, however, was the influence that each substrate material would have on plant physiological responses, substrate redox potential, and overall patterns of Panicum hemitomon biomass allocation.

The spatial and temporal distribution of nutrient resources in a given substrate are known to affect root systems of plants from both nutrient-rich and nutrient-poor habitats (Chapin 1980; Vitousek 1982; de Kroon and Visser 2003). When plants are deficient in key nutrients, important changes in their energy budgets occur, which may in turn influence key biological and chemical interactions between root tissues and the surrounding soil matrix. Boutin et al. (1981) suggested that plants may increase the activity of their extra-cellular phosphatase enzymes when key nutrients are limiting, enabling them to decompose organic phosphates, in turn releasing inorganic ions that can then be taken up by the root. Roots may

also actively alter chemical attributes of the rhizosphere, such as pH (Crawley 2005). Root morphology may also change as a result of spatial and temporal variability in soil nutrient resources. When roots encounter nutrient-rich patches, they may exhibit a proliferative response (Robinson 1994). While there is evidence in support of this (Drew 1975), there is also evidence against (Campbell et al. 1991), suggesting either a non-proliferatory response, or a proliferatory response by roots not encountering nutrient-rich patches. In clonal plants such as Panicum hemitomon, nutrient-rich patches may result in a proliferative of daughter ramets, modifying plant architecture and ultimately nutrient foraging behavior (Evans and Caine 1995). It is therefore important to recognize that considerable variation, or plasticity exists with respect to plant growth responses, particularly that of belowground responses, and that such plasticity, if represented by diminished or depauperate rhizome and root production, could have important implications for floating marsh restoration.

Nutrient availability, substrate redox potential, and interstitial pH are not the only edaphic attributes that influence plant vigor. Chemical oxygen demand (COD) was of concern regarding substrate decomposition and the effect it would have on the quality of the rooting environment, although it is doubtful that COD would be as much of an issue in field settings, such as those slated for thick-mat floating marsh restoration, where stagnant conditions are less likely to occur due to hydrologic exchange with adjacent water bodies. COD, the amount of oxygen required to chemically oxidize a specific quantity of organic matter, is interrelated with hypoxia. In aquatic settings COD and biological oxygen demand (BOD) are related, with COD generally exceeding BOD (APHA 1989). In this study it was assumed that the potential existed for COD to negatively affect Panicum hemitomon growth response via the intensification of already stressful oxygen-limited conditions. I expected such effects to be somewhat accentuated in experimental vessels with constant inundation and poor airing ability.

Although all substrate materials evaluated here were plant-derived, I suspected that each would possess different structural and chemical qualities that would differentially affect the rooting environment, in turn differentially affecting Panicum hemitomom growth response. The same can also be said for each mat or containment material in terms of their respective influence on Panicum hemitomom growth response.

The main objectives in this study were to:

- (1) Determine the degree to which substrate material affects interstitial chemistry and overall Panicum hemitomom growth response and patterns of biomass allocation.
- (2) Determine the degree to which mat or containment material affects interstitial chemistry and overall Panicum hemitomom growth response and patterns of biomass allocation.

Overarching hypothesis:

Panicum hemitomom growth response and patterns of biomass allocation will exhibit significant differences according to substrate and mat or containment materials.

Key hypotheses:

1. In the presence of peat and peat-containing blended substrate materials, as compared to non-peat containing materials, Panicum hemitomom will exhibit:
 - A. Greater above- and belowground production as a result of:
 1. more acidic interstitial pH
 2. less reduced (more normoxic) interstitial conditions
 3. lower COD
 - B. Greater tissue nitrogen content and rates of net CO₂ assimilation
2. In the presence of Duralast coconut fiber mat or containment material, as compared to non-Duralast materials, Panicum hemitomom will exhibit:
 - A. Greater root production as a result of more accommodating interstitial conditions
 - B. Greater above- and belowground production as a result of a more structurally-integrated and stable rooting environment

Materials and Methods

Experimental design

This section describes three separate but inter-dependent experiments (Image 3.1). Experiment – 1 was an evaluation of different planting mediums or substrate materials and their effect on Panicum hemitomon growth response and patterns of biomass allocation. It was initiated in October of 2004, but was prematurely ended eleven months later in September of 2005 as a result of Hurricane Katrina. Early termination refers to the desiccation of all experimental units because recovery did not occur until approximately eight weeks post-Katrina (all experimental units were moved inside a UNO greenhouse prior to landfall to minimize physical disturbance, but adequate watering did not occur). As a result of desiccation, live rhizome and root analyses were not conducted. Experiment – 2 was an evaluation of mat or containment materials and their effect on Panicum hemitomon growth response and patterns of biomass allocation. It was initiated several months after experiment – 1 (May 2005), allowing preliminary findings from experiment – 1 to be incorporated into its design. Experiment – 2 was prematurely ended in October of 2005 for the same reasons as experiment – 1, complications associated with Hurricane Katrina. Experiment – 3, an assessment of substrate COD, was conducted several months after experiments – 1 and 2, and therefore was not affected by Hurricane Katrina. Experiment – 3 was carried out to better understand differences in interstitial water samples, and consequently Panicum hemitomon growth response, as observed over the course of experiment – 1. Experiment – 3 was initiated in February of 2006, and successfully completed six months later in August of 2006.



Image 3.1. Experiment – 1, five months after initiation (top image); experiment – 2, two weeks after initiation (middle image); experiment – 3, two weeks after initiation (bottom image).

Experiment – 1 assessed Panicum hemitomon growth response and patterns of biomass allocation in the presence of 12 different substrate materials, each replicated 5 times for a total of 60 experimental units ($n = 60$). In all, 7 individual substrate or non-blended materials, and 5 combination or blended materials, were tested. All blended substrate materials were combinations of two individual materials each, but as evidenced in the number of treatments, all possible combinations were not tested. Individual substrate materials included: bagasse, cypress mulch, sugarcane leaf strippings, hardwood mulch, ground sphagnum peat moss (referred to as peat hereafter), pine bark mulch, and pine shavings. Blended substrates included: peat and bagasse, cypress mulch and bagasse, hardwood mulch and sugarcane leaf strippings, hardwood mulch and peat, and peat and cypress mulch. Blended substrates consisted of equal amounts (by volume) of each individual substrate used in a given treatment. The 7 individual substrates were all plant-derived and associated with low specific gravity. Peat (Waupaca Northwoods, LLC., Waupaca, WI) was chosen because it most closely resembles the fine-textured, highly-organic substrate of naturally-formed thick-mat floating marsh. Sugarcane leaf strippings and bagasse were included because of interest from the Louisiana Department of Natural Resources (LaDNR) and the Louisiana Department of Environmental Quality (LaDEQ), as well as from independent researchers (Boopathy 2004; Dawson and Boopathy 2007), to identify outlets of use for these materials. Bagasse and sugarcane leaf strippings, both readily available byproducts of the regional sugarcane industry, were obtained from Raceland Sugar Company, Raceland, LA. Bagasse that was one year-old was intentionally chosen over newer material because I thought that older, partially-decomposed material would be more conducive for plant growth. All other materials were chosen because they were plant-derived, lacked mineral content, were inexpensive, and except for the sugarcane leaf strippings and bagasse (which must be acquired from sugarcane mills), were commercially available in southeastern Louisiana.

Each of the 60 experimental units were arranged in a fashion that included a bottom layer of 3 cm thick Duralast coconut fiber (Duralast Products, Memphis, TN), a 25 cm layer of substrate material, and a 3 cm thick top layer of Duralast coconut fiber in this order from bottom to top. An equal amount (by volume) of substrate was added per treatment to ensure that each experimental vessel contained the same amount of rooting medium. I chose to use Duralast coconut fiber as a mat or containment material prior to being experimentally evaluated because it is light-weight, yet rigid and tightly woven, making it especially effective at containing each of the substrates.

One bare-root plug of Panicum hemitomon was planted in the center of each coconut fiber and substrate sandwich (referred to as a vegetated mat hereafter). All plant material was harvested as root and rhizome stock from a single clone growing at the USDA Golden Meadow Plant Materials Center, Galliano, LA. Root and rhizome stock was transported back to the greenhouse facility at the University of New Orleans and propagated for approximately six weeks in 10 cm plastic pots filled with enriched 18-6-12 (N-P-K respectively) Miracle-Gro potting soil (Scotts Miracle-Gro Company, Marysville, OH). Mesic hydrologic conditions were maintained for the entirety of the propagation phase. At transplanting, all potting soil was washed from each plug, and wet weights determined and statistically analyzed to ensure uniformity across treatments. Vegetated mats were positioned in 19-L containers and flooded to a depth of approximately 10 cm above the top layer of Duralast coconut fiber. All experimental vessels were maintained in a fully-exposed outdoor setting, and care was taken to ensure that 10 cm of inundation was maintained for the duration of the experiment.

Experiment – 2 was conducted in a similar fashion to that of experiment – 1, the main exception being that mat or containment material, not substrate, varied across treatments. Commercially available peat (Waupaca Northwoods, LLC., Waupaca, WI) served as the

substrate material based not only on preliminary findings associated with experiment – 1, but because it closely resembles the organic substrate inherent in naturally-formed thick-mat floating marsh. Experiment – 2 was an evaluation of 5 distinct mat materials that are commonly used for erosion control in revegetation projects, each replicated 5 times in a completely randomized fashion for a total of 25 experimental units ($n = 25$). Mat materials included: shredded birch in plastic mesh, burlap, shredded coconut fiber in plastic mesh, Duralast coconut fiber, and wheat straw in plastic mesh. Each experimental vessel included a bottom layer of mat material, followed by a 10 cm layer of peat, culminating with a top layer of mat material, in this order from bottom to top. An equal amount of peat (by volume) was added per treatment to ensure that each experimental vessel contained the same amount of rooting medium. One bare-root plug of Panicum hemitomon was planted in the center of each mat and peat sandwich (again referred to as a vegetated mat hereafter). All plant material for experiment – 2 came from the same lot of propagated plants used in experiment – 1, and as before, plugs were washed of soil, and wet weights determined (and statistically analyzed) prior to planting to ensure uniformity across treatments. All vegetated mats were positioned in 7-L containers and flooded to a depth of approximately 10 cm above the top layer of coconut fiber. All vessels were maintained in a fully-exposed outdoor setting identical to that described for experiment – 1.

Experiment – 3 was an evaluation of the COD associated with each of the 7 individual substrate materials tested in experiment – 1. Two controls (tap water only and Duralast coconut fiber and tap water) were also included. In total, there were 9 treatments, each replicated 5 times in a completely randomized fashion for a total of 45 experimental units ($n = 45$). Each treatment, except for the two controls, included an equal amount of substrate material (by volume) determined using vessel demarcations, and a 3 cm thick top layer of

Duralast coconut fiber. Each treatment was positioned in a 1-L plastic container and placed in a full-transmission greenhouse to minimize extraneous effects associated with precipitation. The dry mass of each experimental unit was determined prior to the onset of the experiment, and final masses were determined at completion, thus allowing for the calculation of substrate dry-mass loss due to decomposition. This was done post-hoc as a means for elucidating, to the extent possible, differences in substrate decomposition associated with experiment – 2.

Experiment – 3 did not include a vegetative component.

The fertilization regime applied in all three experiments was based on peak mean annual nitrogen and phosphorous outflow loading rates ($8.9 - 23.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $0.9 - 2.0 \text{ g P m}^{-2} \text{ yr}^{-1}$ respectively) as reported by Lane et al. (1999) from the Caernarvon diversion, Caernarvon, LA. Loadings for both nitrogen and phosphorous ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $2 \text{ g P m}^{-2} \text{ yr}^{-1}$ respectively) were achieved using slow-release granular Osmocote fertilizer (Scotts Miracle-Gro Company, Marysville, OH), with a guaranteed analysis of 18-6-12 (N-P-K respectively).

Edaphic data

Substrate redox potential was measured bi-monthly over the course of experiments – 1 and 2, but only twice over the course of experiment – 3, as a means for assessing the overall quality of the rooting environment (Gambrell and Patrick 1978; Gambrell et al. 1991). Redox potential was always measured using three probes per vessel, each inserted to a depth of approximately 5 cm for experiment – 2, and to a depth of approximately 10 cm for experiments – 1 and 3. Platinum-tipped probes were constructed according to the method described by Faulkner (1989), and were brightened and calibrated prior to each use. Upon insertion, probes were allowed to equilibrate for approximately 0.5 hours, after which readings were taken using a hand-held Hanna model HI-9025 millivolt meter (Hanna Instruments, Woonsocket, RI) and a

KCL saturated calomel reference electrode. Each raw value was adjusted by +244 mV for the calomel reference electrode that was used (Faulkner 1989).

Interstitial pH was measured monthly over the course of experiment – 1, and bi-monthly over the course of experiment – 2, also as a means for assessing the quality of the rooting environment, as pH can differ markedly across substrate types, or as in this case, across substrate materials. Samples were withdrawn using an interstitial water sipper according to methods described by McKee et al. (1988), and measured using a hand-held Corning 313 pH/mV meter (Corning Instruments, Fairport, NY).

Interstitial water samples used for chemical oxygen demand (COD) were withdrawn on seven occasions over the course of experiment – 3 (weeks 1 - 4, 6, 8, and 20), and stabilized using 2 drops of nitric acid per 20 ml of sample solution. Samples were first refrigerated, and then transported (on ice) to Nichols State University in Thibodaux, LA, for processing and analysis. Interstitial pH for experiment – 3 was measured during each COD sampling using an interstitial water sipper as in experiment – 2.

Shoot data

Cumulative stem height, the total height of all live stems emerging from the surface of each vegetated mat, was measured monthly over the duration of experiments – 1 and 2. As before, measuring cumulative stem height also allowed for the determination of total stem height, total stem number, and mean stem height. The partitioning of stem material into live and dead components was not possible for experiment – 1 or 2 because all plant material was dead when post-Katrina recovery occurred.

Panicum hemitomon net CO₂ assimilation for experiment – 1 was measured using a Li-Cor 6400 portable photosystem (Li-Cor, Lincoln, NE). Measurements were performed on two fully-expanded leaves per experimental unit, generally the second and third leaves from the

terminal leaf of each plant. All measurements were performed under light-saturated conditions [$1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR)] with reference CO_2 levels set at 370 ppm. Each leaf on which photosynthetic measurements were performed was subsequently clipped and oven-dried at 60°C for approximately five days, or until a constant mass was attained. Afterward, each leaf was ground using a Wiley Mill to allow for carbon-hydrogen-nitrogen (CHN) analysis. CHN results were used in conjunction with leaf mass:area ratios and photosynthetic results to determine leaf tissue nutrient content and plant photosynthetic nitrogen-use efficiency (PNUE).

Harvested biomass

Biomass from experiment – 1 was harvested in September of 2005 after eleven months of growth. Biomass from experiment – 2 was also harvested in September of 2005, but after only five months of growth. Although exact assessment of aboveground biomass was possible for experiments – 1 and 2, exact assessment of belowground biomass was only obtainable from experiment – 2 because several treatments in experiment – 1 unexpectedly lost mass over the course of the experiment. This loss is attributed to the combined effects of marginal plant growth and substrate decomposition, as it was obvious upon visual inspection that Panicum hemitomom rhizome and root growth associated with some substrate materials was so poor that the mass of material lost to decomposition did not need to be excessive to have this effect. Therefore, belowground biomass totals for experiment – 1 have been interpreted as total change in biomass values because it was not possible to accurately distinguish between the individual effects of substrate decomposition and belowground biomass. Ultimately, all belowground biomass, and substrate and mat or containment material, for each experimental vessel in experiments – 1 and 2 was placed in labeled paper bags and dried at 60°C until a constant mass was attained. Pre-weights were subtracted from final weights to determine

either total change in biomass, as in experiment – 1, or actual belowground biomass, as in experiment – 2.

Statistical analyses

SAS Version 9.1 (SAS Institute, Cary, NC) was used for all statistical analyses reported herein. All variables were evaluated independently to ensure that each clearly met the normality and heteroscedasticity assumptions associated with analysis of variance (ANOVA). A two-way ANOVA using the SAS PROC GLM procedure was used to test for differences in all non-sequentially measured variables. A multivariate repeated measures analysis of variance (MANOVA), also using the SAS PROC GLM procedure, was used to test for differences among sequentially measured variables. A significance level of $\alpha = 0.05$ was used for all statistical tests unless specified otherwise. For tests of significance associated with MANOVA outputs, preference was given to Wilk's lambda when test of significance values did not differ. When differences did exist, preference was given to Pillai's trace because of its robustness to violations of assumptions (Kleinbaum et al. 1998; Scheiner and Gurevitch 2001). Only ecologically significant post-hoc test results are included in the Results section. Other post-hoc tests, when performed, are reported in the Appendix.

Results

Edaphic data

Substrate redox potential for experiment – 1 (Figure 3.1, top and bottom panels) decreased over time for nearly all treatments (Wilk's lambda: $F_{5,44} = 136.04$, $p < 0.0001$). Although not statistically significant, redox potentials were somewhat greater (i.e., less reduced) for peat and peat-containing blended substrates. The rate of decline in redox potentials over the course of the experiment varied significantly across substrates (Pillai's trace: $F_{55,240} = 1.47$, $p < 0.0257$), with bagasse, sugarcane leaf strippings, and pine shavings attaining highly-reduced levels (i.e., redox values < 100 mV). In contrast, redox potentials for peat and peat-containing blended substrates never reached such low levels, not even by the completion of the experiment as evident in the August 2005 data. However, the level of reduction in these less-reduced treatments was still below that which is usually associated with normoxic conditions (+400 mV), suggesting mild oxygen limitation.

Interstitial pH for experiment – 1 (Appendix, Figure 3) increased significantly over the course of the experiment (Wilk's lambda: $F_{5,44} = 253.9$, $p < 0.0001$), in some cases by as much as two pH units. The rate of increase also varied according to substrate (Pillai's trace: $F_{55,240} = 2.53$, $p < 0.0001$), with initial differences, equilibrating and becoming more neutral over time.

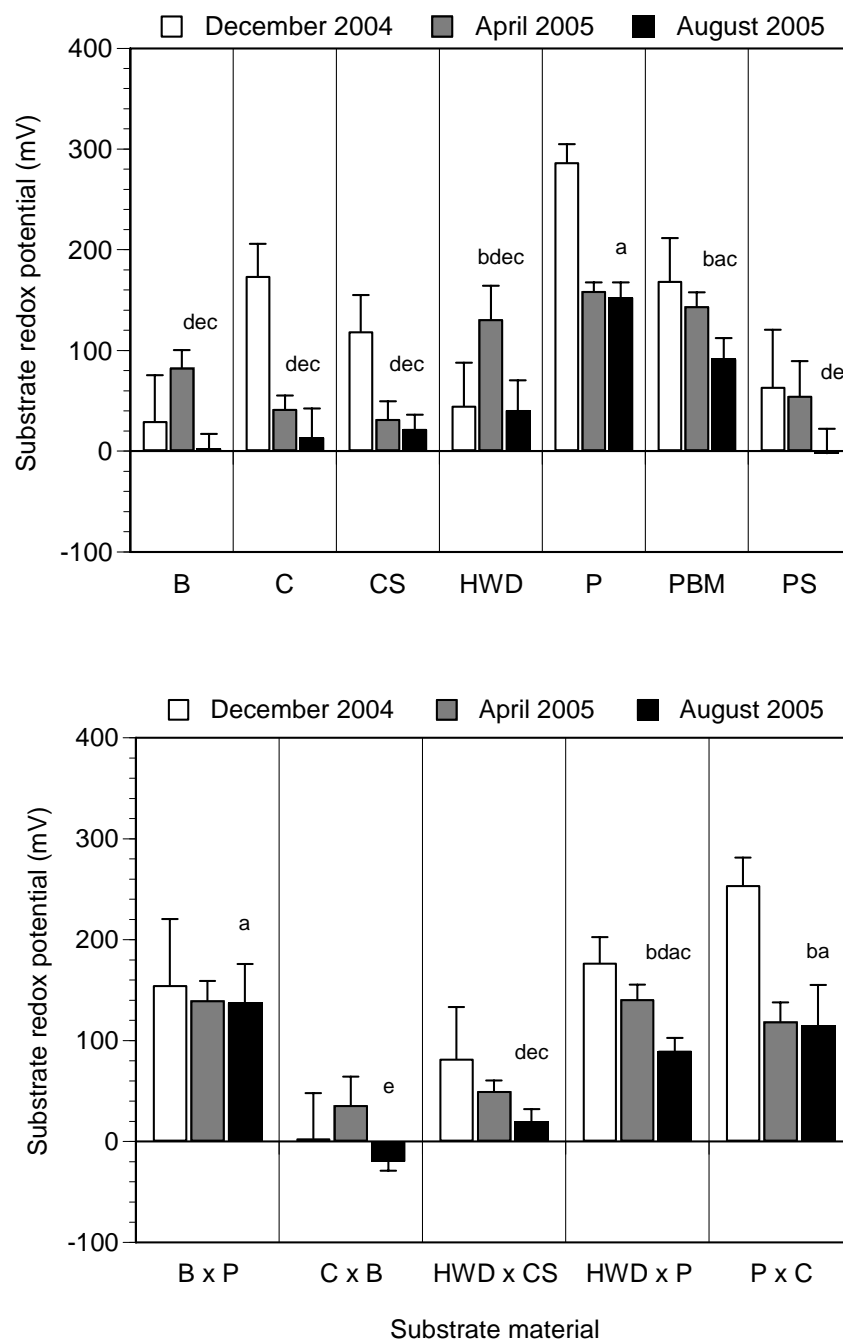


Figure 3.1. The effect of individual (top panel) and blended (bottom panel) substrate material on substrate redox potential (mV) for experiment – 1, measured monthly over a nine-month period. Treatment codes are as follows: B = bagasse; C = cypress mulch; CS = sugarcane leaf strippings; HWD = hardwood mulch; P = peat; PBM = pine bark mulch; PS = pine shavings; B x P = bagasse and peat; C x B = cypress mulch and bagasse; HWD x CS = hardwood mulch and sugarcane leaf strippings; HWD x P = hardwood mulch and peat; P x C = peat and cypress mulch. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for August 2005 data only ($F_{11,168} = 8.93$, $p < 0.0001$).

Substrate redox potential for experiment – 2 (Figure 3.2) varied according to mat or containment material at the beginning of the experiment, but by August, redox potentials roughly equilibrated, all converging on values between 100 and 150 mV. Within treatment variation obscured any among treatment statistical significance, although a significant interaction between measurement time and mat or containment material was observed (Wilk's Lambda $F_{4,20} = 5.75$, $p = 0.0030$). Although significant, no ecologically important patterns were observed. Mat or containment materials associated with the most reduced conditions shortly after initiation in June, such as birch, and to a lesser extent straw, became some of the least reduced by August.

Interstitial pH for experiment – 2 (Appendix, Figure 4) increased significantly over time for most mat or containment materials ($F_{1,20} = 5.81$, $p = 0.0257$). The time by treatment interaction was not significant.

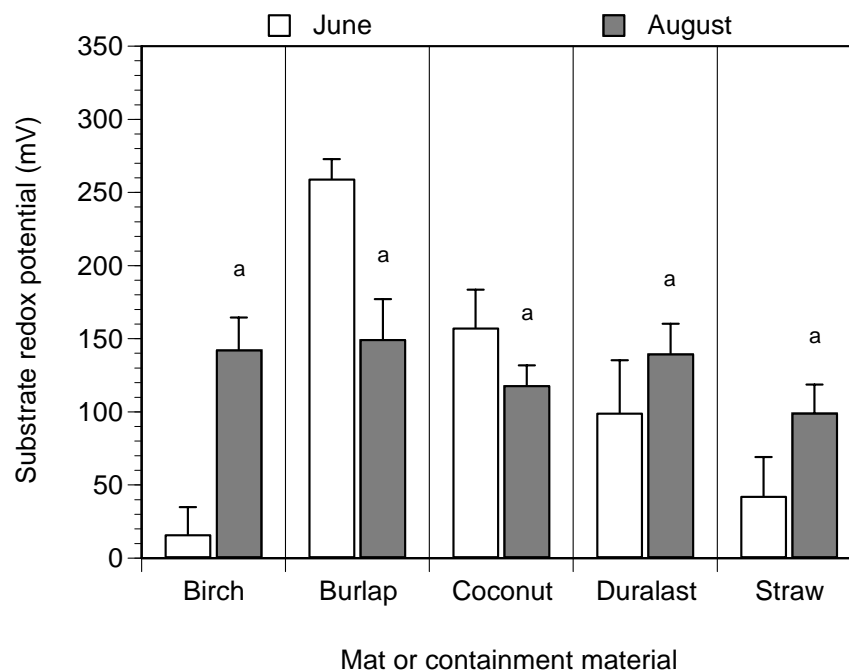


Figure 3.2. The effect of mat or containment material and peat substrate on substrate redox potential (mV) for experiment – 2. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for August 2005 data only ($F_{4,20} = 0.97$, $p = 0.4440$).

Substrate redox potential for experiment – 3 (Figure 3.3) decreased significantly over time for most treatments ($F_{1,36} = 7.11$, $p = 0.0114$), with peat representing the largest decrease (nearly 250 mV). Redox values for all treatments tended to converge on values between +200 to +400 mV, the exception being bagasse, which attained greater reduction at +180 mV. Within treatment variation in these data overshadowed among treatment statistical significance, resulting in a non-significant time by treatment interaction. Redox potentials for all treatments were reduced enough to be associated with moderate hypoxia (i.e., between +200 and +400 mV).

Interstitial pH for experiment – 3 (Appendix, Figure 5) increased significantly for all treatments over the course of the experiment (Wilk's lambda: $F_{3,34} = 1384.38$, $p < 0.0001$), by as much as three pH units for treatments such as bagasse and cypress mulch. Interstitial pH for peat changed the least, although still increasing by two pH units. The rate of increase in interstitial pH over the course of the experiment also differed among treatments (Pillai's trace: $F_{21,108} = 4.01$, $p < 0.0001$). Overall, interstitial pH for experiment – 3 became more alkaline over time, the exceptions being peat, and to a lesser degree, pine bark mulch, which tended to remain slightly acidic.

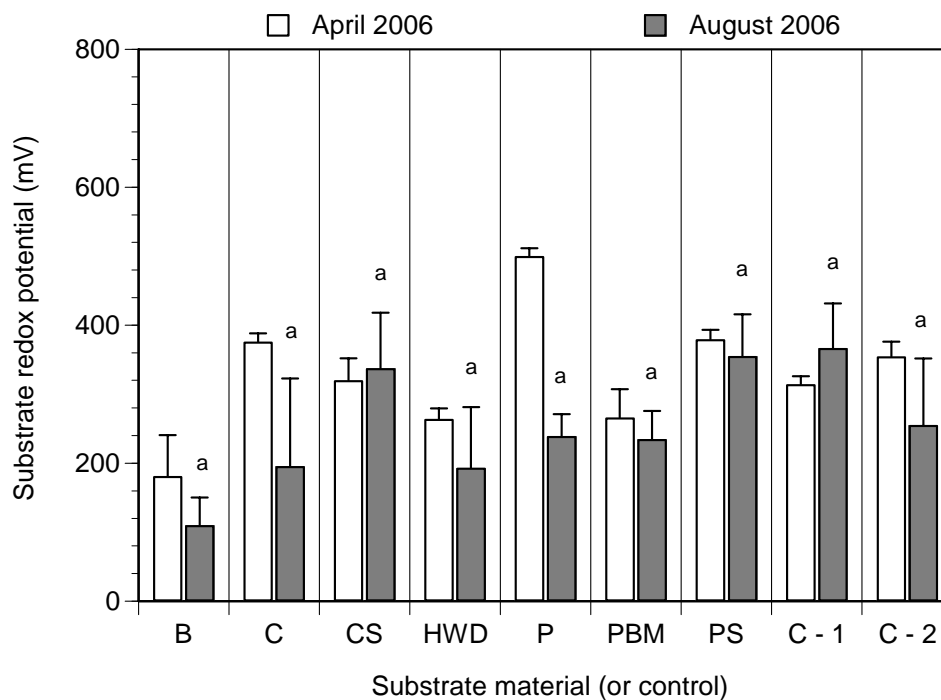


Figure 3.3. The effect of substrate material on substrate redox potential (mV) for experiment – 3. Treatment codes are as follows: B = bagasse; C = cypress mulch; CS = sugarcane leaf strippings; HWD = hardwood mulch; P = peat; PBM = pine bark mulch; PS = pine shavings; C – 1 = tap water; C – 2 = tap water and Duralast coconut fiber. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for August 2006 data only ($F_{8,36} = 1.27$, $p = 0.2915$).

COD for experiment – 3 (Figure 3.4) decreased significantly over the course of the experiment (Wilk's lambda: $F_{3,34} = 1388.25$, $p < 0.0001$), but by completion (i.e., Week 20), no significant treatment effects were observed. Despite the fact that COD for all treatments converged on 200 to 300 mg/L by Week 20, the rate of decline in COD over the 20-week period differed significantly among materials (Pillai's trace: $F_{24,99} = 10.73$, $p < 0.0001$). Initially, peat and cypress mulch exhibited the lowest COD, whereas pine bark mulch and pine shavings exhibited the greatest.

Decomposition of those substrates tested in experiment – 3 (Appendix, Figure 6) varied significantly with respect to treatment ($F_{8,44} = 725.98$, $p < 0.0001$), ranging from 25.5 g (sugarcane leaf strippings) to 82.0 g (hardwood mulch) of loss of dry biomass.

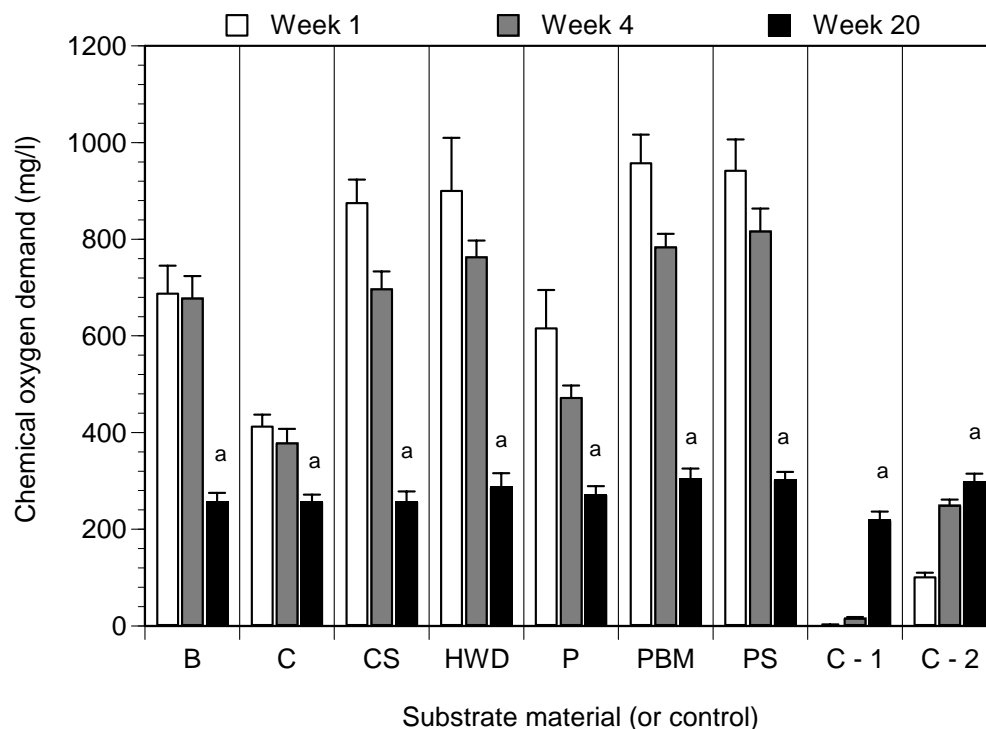


Figure 3.4. The effect of substrate material on COD for experiment – 3. Treatment codes are as follows: B = bagasse; C = cypress mulch; CS = sugarcane leaf strippings; HWD = hardwood mulch; P = peat; PBM = pine bark mulch; PS = pine shavings; C – 1 = tap water; C – 2 = tap water and Duralast coconut fiber. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for week-20 data only ($F_{8,36} = 2.19$, $p = 0.0517$).

Shoot data

Panicum hemitomom cumulative stem height for experiment – 1 (Figure 3.5) increased significantly for all substrates over the course of the experiment (Wilk's lambda: $F_{9,40} = 116.92$, $p < 0.0001$). However, the rate of increase in cumulative stem height differed significantly among substrates (Pillai's trace: $F_{99,432} = 1.72$, $p < 0.0001$), with peat and peat-containing blended materials exhibiting the greatest rates of increase. Overall, cumulative stem heights were greatest in conjunction with peat and peat-containing blended substrate materials, and the least for plants grown in bagasse and cypress mulch. Of the two sugarcane byproducts, leaf strippings were associated with greater Panicum hemitomom cumulative stem height as compared to bagasse, but still less than peat-based materials.

Panicum hemitomom net CO₂ assimilation, photosynthetic nitrogen-use efficiency, and PNUE for experiment – 1 (Appendix, Table 10), all exhibited non-significant treatment effects. Alternatively, total stem number, total stem height, and mean stem height (Appendix, Table 11), all exhibited highly significant treatment effects. Peat and peat-containing blended substrate materials resulted in the most vigorous Panicum hemitomom growth as gathered from these stem metrics.

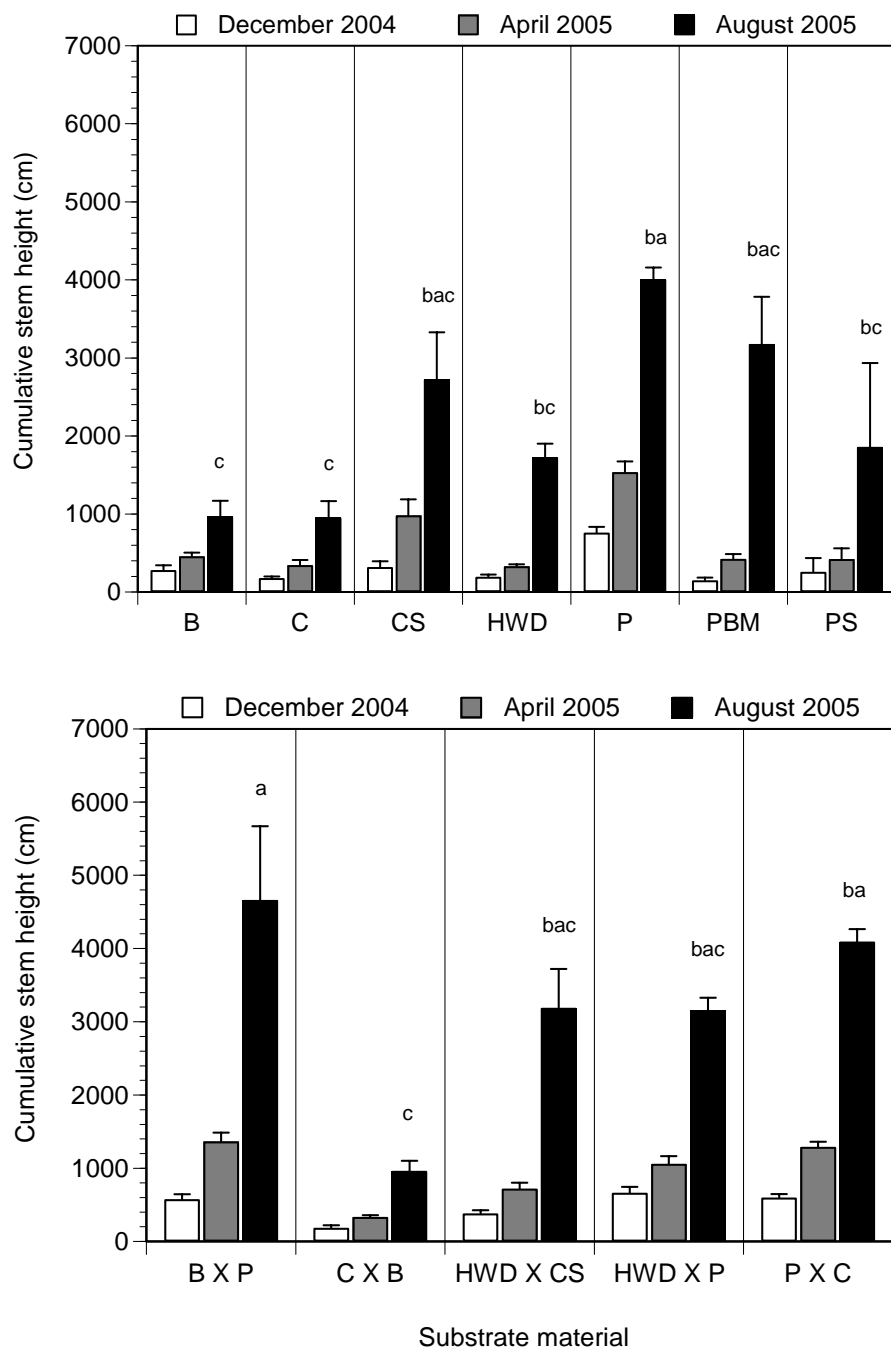


Figure 3.5. The effect of individual (top panel) and blended (bottom panel) substrate material on *Panicum hemitomon* cumulative stem height (cm) for experiment – 1, measured monthly over an eleven-month period. Treatment codes are as follows: B = bagasse; C = cypress mulch; CS = sugarcane leaf strippings; HWD = hardwood mulch; P = peat; PBM = pine bark mulch; PS = pine shavings; B x P = bagasse and peat; C x B = cypress mulch and peat; HWD x CS = hardwood mulch and sugarcane leaf strippings; HWD x P = hardwood mulch and peat; P x C = peat and cypress mulch. Values are means \pm SE (n = 5). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for August 2005 data only ($F_{11,48} = 6.06$, $p < 0.0001$).

Panicum hemitomom cumulative stem height for experiment – 2 (Figure 3.6) increased significantly over the course of the experiment for all mat or containment materials (Wilk's lambda: $F_{2,19} = 554.6$, $p < 0.0001$). The rate of increase in cumulative stem height also differed significantly across materials (Pillai's trace: $F_{8,40} = 5.33$, $p < 0.0001$). The most notable effect was the small cumulative stem height exhibited by plants grown in shredded birch, and to a lesser extent, in straw, whereas plants grown with all other mat or containment materials exhibited greater cumulative stem heights. Burlap was associated with the greatest cumulative stem height.

Total stem height, total stem number, and mean stem height associated with experiment – 2 (Appendix, Table 12) also varied significantly according to mat or containment material. Shredded birch, and to a lesser extent straw, exhibited fewer and shorter stems. Burlap was associated with the greatest number of stems and the greatest total stem height, whereas coconut in plastic mesh was associated with the greatest mean stem height.

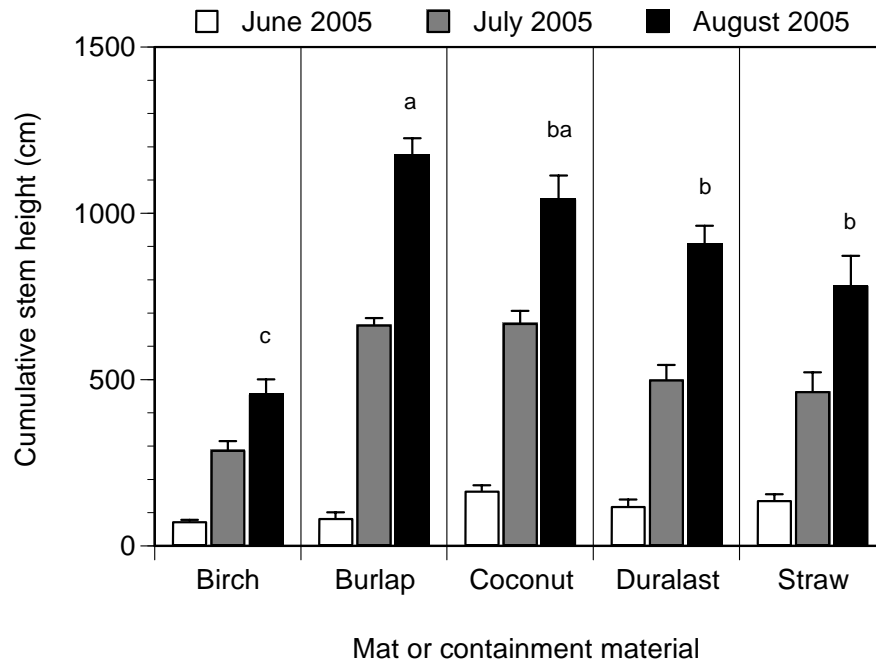


Figure 3.6. The effect of mat or containment material on *Panicum hemitomon* cumulative stem height (cm) for experiment – 2, measured monthly over a three-month period. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for August 2005 data only ($F_{4,20} = 19.26$, $p < 0.0001$).

Harvested biomass

Panicum hemitomom total biomass (or amount change) for experiment – 1 (Figure 3.7) varied significantly according to substrate material ($F_{11,48} = 7.67$, $p < 0.0001$). Peat and peat-containing blended substrate materials, and to a lesser degree, sugarcane leaf strippings and pine bark mulch, were associated with the greatest aboveground production. In contrast, Panicum hemitomom grown in bagasse and cypress mulch exhibited the least aboveground production. Belowground biomass (or amount change) also varied significantly with respect to substrate material ($F_{11,48} = 7.67$, $p < 0.0001$). Panicum hemitomom grown in conjunction with peat or peat-containing blended substrates exhibited the greatest belowground biomass (Image 3.2), although not in all cases as evident by the negative values associated with bagasse and peat and hardwood mulch and peat. Substrates exhibiting negative amount-change values, such as bagasse and hardwood mulch, were associated with greatly reduced Panicum hemitomom rhizome and root growth.

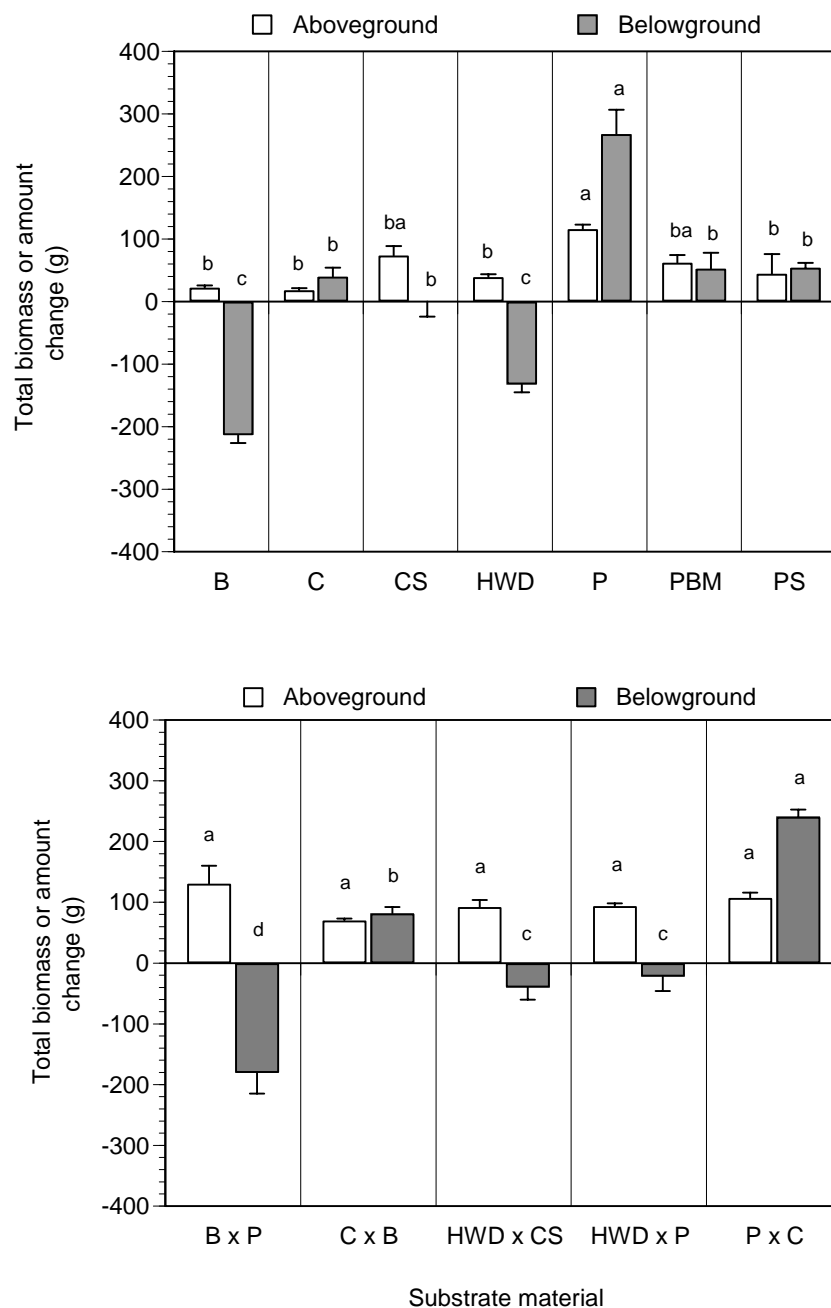


Figure 3.7. The effect of individual (top panel) and blended (bottom panel) substrate material on *Panicum hemitomon* total biomass (g) for experiment – 1, measured as dry biomass for aboveground biomass and as amount change for belowground biomass. Treatment codes are as follows: B = bagasse; C = cypress mulch; CS = sugarcane leaf strippings; HWD = hardwood mulch; P = peat; PBM = pine bark mulch; PS = pine shavings; B x P = bagasse and peat; C x B = cypress mulch and peat; HWD x CS = hardwood mulch and sugarcane leaf strippings; HWD x P = hardwood mulch and peat; P x C = peat and cypress mulch. Values are means \pm SE (n = 5). Letters over bars represent significantly different means (Tukey's pairwise comparisons, α = 0.05) for above- ($F_{11,48} = 6.29$, $p < 0.0001$) and belowground biomass ($F_{11,48} = 45.86$, $p < 0.0001$) analyzed separately.



Image 3.2. Image of visible rhizome and root biomass for experiment – 1 for pine shavings (top image) and peat (bottom image). Note that while peat-containing treatments were most conducive for *Panicum hemitomon* growth, pine shavings, despite the paucity of visible biomass in this image, was not associated with the poorest growth.

Panicum hemitomom above- and belowground biomass for experiment – 2 (Figure 3.8) varied significantly according to mat or containment material ($F_{4,20} = 7.67$, $p < 0.0001$ and $F_{4,20} = 3.52$, $p = 0.0250$ respectively). Overall, partitions of biomass were relatively uniform across mat or containment materials, the exceptions being biomass associated with shredded birch, and to a lesser extent, with straw (at least for aboveground biomass). The greatest aboveground biomass was associated with burlap, whereas the greatest belowground biomass was associated with Duralast coconut fiber.

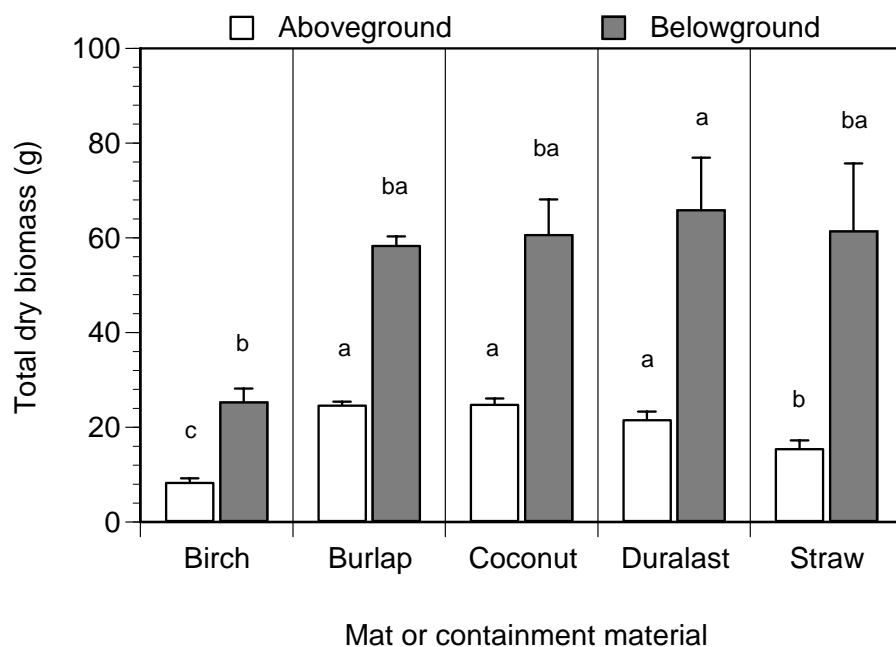


Figure 3.8. The effect of mat or containment material on *Panicum hemitomon* above- and belowground biomass (g) for experiment – 2. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for above- ($F_{4,20} = 34.47$, $p < 0.0001$) and belowground biomass ($F_{4,20} = 3.52$, $p = 0.0250$) analyzed separately.

Discussion

The experiments described in this chapter provide useful data, although admittedly cursory in some instances, with respect to Panicum hemitomon growth response as influenced by substrate and mat or containment materials. Such materials are required for floating marsh restoration because they provide both the planting medium and the structural support initially required for Panicum hemitomon establishment. Peat and peat-containing blended substrate materials were associated with edaphic conditions that promoted vigorous Panicum hemitomon growth (i.e., less reduced conditions, lower COD, and slightly acidic pH). Incidentally, and not mentioned prior, Panicum hemitomon-dominated floating marshes generally exhibit slightly acidic pH because of the highly-organic substrates (Sasser 1994). Although incorporating bagasse or sugarcane leaf strippings into the floating marsh restoration protocol does not appear overly beneficial at this point, it is possible that byproducts from other plant-fiber industries could be used for such applications. With the exception of the shredded birch treatment, there was little variation in plant response across mat or containment material. Duralast coconut fiber appeared best not only because it was associated with relatively vigorous Panicum hemitomon growth, but because it was structurally rigid and naturally buoyant, as well as capable of containing fine-textured substrates, such as peat, upon submergence.

Plant vigor and the partitioning of biomass to above- and belowground components are directly influenced not only by light and moisture regimes, but by site-specific plant stressors and edaphic characteristics (Chapin 1980; Lambers et al. 1998). This is especially important with respect to wetland restoration, as there is generally a need to foster conditions that result in immediate, and vigorous, plant growth in lieu of particular time-sensitive objectives and goals. Although there are some commonalities, restoring thick-mat floating marsh presents different structural and ecological challenges as compared to more typical wetland restoration

because of the need to create an intact and buoyant root mat. Although floating marsh restoration does not require much in the way of site preparation, a substrate of low specific gravity that supports vigorous Panicum hemitomon growth is required. Therefore, I set out to identify substrate and mat or containment materials that would have a minimal negative effect on buoyancy, as well as materials that would promote vigorous Panicum hemitomon growth. Based on experimental findings reported herein, peat or peat-containing blended substrate materials (i.e., those containing $\geq 50\%$ peat content by volume), and Duralast coconut fiber mat or containment material, are the materials of choice.

Panicum hemitomon growth was more vigorous in the presence of peat and peat-containing blended substrate materials, partly because Panicum hemitomon appears tolerant of slightly acid pH (pH ranging from 5 to 7), but also because these materials were associated with less reduced (less hypoxic) conditions. Soils generally become oxygen-limited or hypoxic within several hours, to a few days, after flooding because oxygen consumption belowground occurs at very high rates, with plant roots respiring at rates faster than shoots (Amthor 1989), and rates of the microbial community faster still (Paul and Clark 1996). Oxygen demands are further accentuated by the slow diffusion of oxygen in aqueous solutions, at times 10^{-4} the rate as in air-filled pores (Armstrong 1982; Epstein and Bloom 2005). Although wetland-adapted plants possess specific adaptations for tolerating flooding, they nevertheless incur stress, the degree to which is generally species dependent (Cronk and Fennessey 2001). Such stressors may at least partially explain the poor performance of Panicum hemitomon grown in non peat-containing substrate materials, such as hardwood mulch and bagasse. Substrates that were indicative of more reduced conditions were also associated with greater COD. COD is inter-related with redox potential, in that higher COD equates to less biologically available oxygen, and therefore a greater potential for oxygen deficiency (Gambrell and Patrick 1978; Richardson

and Vepraskas 2001). If the level of reduction was the main factor affecting the growth response of Panicum hemitomom, then the differences observed in growth response suggest that Panicum hemitomom does not have an exceptionally high tolerance for oxygen limitation because differences in redox potentials, such as those between peat and hardwood mulch, were not that great (i.e., ± 150 mV). Perhaps cumulative effects of COD and redox potential, along with some degree of nutrient immobilization by substrate-specific microbial communities, were influencing the patterns as observed.

Epstein and Bloom (2005) provide some insight into several of the substrate materials tested here in terms of general characteristics. They suggest that peat-based substrates are generally acidic, known to release organic substances over time, and are largely beneficial for ion exchange. Bark on the other hand, regardless of whether conifer or hardwood-derived, has low water-holding capacity, immobilizes nitrogen, and must be aged to diminish toxic content. Sawdust, represented in this study by pine shavings, is generally associated with poor nutrient content, and depending on source, alkaline pH (Epstein and Bloom 2005). In reference to sugarcane leaf strippings, and to a lesser extent for bagasse, it is common in intensively-cultivated agricultural settings in Louisiana for sugarcane to be sprayed prior to harvest with glyphosate defoliating and ripening compounds (LSU Ag Center 2001), such as PALADO-L (Monsanto Company, St. Louis, MO). While no definite confirmation underlies this assertion, if fields from which sugarcane leaf strippings (and bagasse) were obtained were sprayed with a ripening agent, it is possible that residues were present, and may at least partially account for the poor Panicum hemitomom growth response associated with these two materials.

When Panicum hemitomom growth response as influenced by mat or containment material is considered independent of substrate material, it is important to note that differences in plant response can be solely attributed to each mat or containment material because

conditions in each experimental vessel were otherwise identical. Panicum hemitomon biomass was fairly uniform across four of the five mat or containment materials, the main exception being shredded birch, and to a lesser extent, straw. Potential explanations for this discrepancy in plant response are attributed to inherent qualities of the birch material, such as those reasons mentioned earlier in reference to wood or bark-based materials. This material, which appeared to be shredded birch wood, likely had a high carbon:nitrogen ratio (C:N), as most wood fiber does (Barnes et al. 1998). A high C:N ratio could enhance nutrient limitation from the perspective of the plant because a greater proportion of the nutrient pool would be sequestered by the microbial community for organic matter decomposition (Barnes et al. 1998; Badalucco and Kuikman 2001). Substrate redox potential would also tend to decrease under such circumstances. It is also possible, however, that birch wood possesses some chemical attribute that negatively affects or suppresses plant growth. It is not known whether such effects were influential here because neither of these potential theories was pursued in sufficient detail because doing so was beyond the scope of this research.

For floating marsh restoration to be as successful as possible, it is important to provide conditions that are initially as accommodating as possible for Panicum hemitomon establishment and growth. Therefore, preference should be given to materials such as peat or peat-containing blended substrates, as opposed to materials that become favorable only after a significant time lag. For large-scale floating marsh restoration, costs of materials is an additional consideration that must be taken into account because, as encountered with this research, Duralast coconut fiber, the superior mat or containment material, was also the most expensive. Resource managers must therefore weigh potential trade-offs in cost-savings in terms of rapid plant establishment and potential resilience to disturbance.

Chapter 4

Assessment of Multi-species Effects and Establishment Techniques on Panicum hemitomon Growth Response and Overall Floating Marsh Vegetative Development

Introduction

Primary objectives

The primary objectives of this large-scale, controlled-setting experiment were to: (1) elucidate Panicum hemitomon growth response and patterns of biomass allocation, and overall created floating marsh vegetative development as influenced by competitive interactions, using a multi-species approach; (2) evaluate growth response and morphological attributes of several laterally-growing plant species, and determine which, if any, possessed attributes that would enhance overall mat structural integrity and buoyancy; (3) evaluate these same laterally-growing plant species with respect to their potential to increase coalescence among created mats if in a field setting, while simultaneously determining their potential to facilitate the establishment of Panicum hemitomon; and (4) evaluate, in a cursory sense, a suite of techniques for augmenting Panicum hemitomon establishment, potentially enhancing the cost-effectiveness of floating marsh restoration.

For thick-mat floating marsh restoration, as with most wetland restoration projects, the overarching objective is for the desired vegetation to become established as quickly and as effectively as possible. Reasons for this include, but are not limited to, increased resistance and resilience to physical disturbance, increased resistance of vegetated settings, or in this case vegetated mats, to the colonization of unwanted opportunistic plant species, and the need to create the habitat-providing services that most wetland restoration projects are evaluated by (Zedler 2001; Perrow and Davy 2002; Falk et al. 2006). Because the ecological knowledge

required to adequately assess different methods for restoring floating marsh, much less data pertaining to avenues for enhancement as described above, were insufficient at the time, I implemented and conducted this large-scale, controlled-setting experiment.

Building upon data generated in earlier experiments (as reported herein, Chapters 2 and 3), this experiment was designed to elucidate Panicum hemitomon growth response and patterns of biomass allocation within a framework in which two distinct approaches for creating thick-mat floating marsh could be simultaneously evaluated. The first was a multi-species planting approach targeting floating marsh vegetative development by combining different laterally-growing edge species with Panicum hemitomon, all using a standardized establishment technique. The second was simply an assessment of different Panicum hemitomon establishment techniques. I saw value in the multi-species approach, the primary objective of this research, because it allowed for a thorough assessment of Panicum hemitomon growth response as influenced by competitive interactions, while simultaneously aiding in the identification of those secondary species that had the greatest potential to bolster root mat structural integrity and buoyancy.

Background

In addition to the actual restoration, wetland restoration projects afford scientists and resource managers the opportunity to test and evaluate innovative techniques and approaches that appear promising with respect to achieving project-specific objectives, but have yet to be rigorously tested. Conducting this experiment under controlled conditions allowed me to test innovative and/or previously untested ideas, thereby identifying not only obstacles that could compromise more costly field-based evaluations, but also identifying potentially beneficial techniques worthy of greater study.

Recent advances in ecological restoration in both terrestrial and wetland settings have demonstrated that multi-species planting approaches may enhance overall restoration success if the species employed exhibit different growth forms, but even more so, if different functional groups are represented (Ewel 1997; Hooper and Vitousek 1997; Whisenant 1999; McKee et al. 2007). As opposed to species-specific morphological differences, functional group diversity, such as nitrogen-fixing legumes, species with symbiotic mycorrhizal associations, or annual versus perennial species with different life history traits, may alter environmental conditions, and in some cases, physical or structural site attributes, in ways that ultimately facilitate the establishment of other, or later-arriving species. For example, Zedler et al. (2001) and Callaway et al. (2003) demonstrated in the Tijuana estuary that soil nitrogen concentration, soil organic matter, and total plot biomass could all be increased by including the halophyte Salicornia virginica L. in the planting protocol. Interestingly, such gains were achieved regardless of whether Salicornia virginica was planted with or without other species, but if omitted from the planting protocol, less beneficial results were observed. In a more recent study, McKee et al. (2007) demonstrated in a clear-cut coastal forest in Belize that Sesuvium portulacastrum (L.) L. and Distichlis spicata (L.) (Greene), two herbaceous species, benefited mangrove recruitment by way of greater propagule entrapment, enhanced seedling structural support, and the amelioration of soil temperature and aeration ability. Among other findings, these two studies demonstrate that certain species may disproportionately benefit, whether directly or indirectly, wetland restoration efforts more so than others. Although no such studies have been carried out explicitly with floating marsh restoration in mind, such facilitation has generally been described in floating marshes of the Okavango delta of Botswana (Ellery et al. 1990). The elucidation of avenues for augmenting Panicum hemitomon establishment in thick-mat floating marsh is needed because wetland restoration projects, as this one is, are often

evaluated using criteria that are vegetation based and time specific (Whisenant 1999; Zedler 2001; Perrow and Davy 2002; SERI 2002; Falk et al. 2006). I envisioned that a multi-species approach would result in a more effective means for restoring thick-mat floating marsh, and a reduction in both the cost associated with the restoration, as well as the time it takes for particular benchmarks of success to be achieved.

A fundamental concept of assessing wetland restoration success is the identification of parameters by which progress can be measured (SERI 2004). Implementing approaches that ameliorate inhibitory abiotic and biotic parameters, or approaches such as companion planting that take advantage of species that exhibit a capacity for coexistence, are generally preferable, but not always feasible, because of site-specific physical characteristics and/or associated alternative states (Whisenant 1999; McKee et al. 2007). As demonstrated in wetland ecosystems, multi-species plantings and their increased ability to influence important ecosystem-level processes represent one approach that may be advantageous under some circumstances. In addition to those benefits noted earlier, species diversity has been linked to increased productivity (Naeem et al. 1994), nutrient retention (Ewel et al. 1991), ecosystem resilience, resistance, and reliability (D'Antonio and Vitousek 1992; Tilman and Downing 1994; Johnson et al. 1996; Naeem and Li 1997), and decreased invasibility by other species (Tilman 1997; Symstad 2000). I envisioned that similar, but more floating marsh-specific benefits, could be achieved for floating marsh restoration by implementing a multi-species approach, realizing that such benefits may be difficult to recognize in a non-field setting, or within the time frame allowed for this experiment to be conducted. Hence, this experiment may be best interpreted as a non-field trial that may, depending on temporal and monetary constraints, result in the identification of a means for enhancing floating marsh restoration.

As described earlier, large-scale floating marsh formation results from deltaic subsidence and increased marsh water levels (O'Neil 1949). Alternatively, secondary formation is generally associated with the lateral advancement of the marsh edge into open water, or areas that are otherwise unvegetated (Russell 1942). This advancement is typically achieved by laterally-growing edge species (and to a lesser extent by Panicum hemitomon) that exhibit extensive and rapid rhizome or stolon growth, or by species that otherwise have a propensity for colonizing open water habitats. Such growth strategies not only have the potential to advance the marsh vegetative front, but equally as important, may partly be responsible for establishing a preliminary root network that facilitates Panicum hemitomon establishment. As a result, I was interested in elucidating the influence of laterally-growing edge specialists on Panicum hemitomon growth response and patterns of biomass allocation, as well as developing a better understanding of how such species may influence overall floating marsh vegetative development.

Ecological benchmarks for assessing progress, or for measuring wetland restoration success, are generally project specific, but often include standard measures such as plant biomass, soil nutrient concentrations, organic matter content, seedling establishment and survivorship, or simply measures of species richness or diversity (Zedler 2001; Whisenant 1999; Falk et al. 2006; McKee et al. 2007). Despite their usefulness elsewhere, other metrics were required to meaningfully assess thick-mat floating marsh being created under non-field conditions. I wanted to identify parameters that would not only be useful under controlled conditions, but equally as important, also adoptable in some capacity for field-based assessments. The parameters I chose included: total mat biomass, Panicum hemitomon total and component-specific biomass, the proportion of total area vegetated taking into account

individual and multi-species contributions, Panicum hemitomom total rhizome length, and root specific gravity for each species.

This experiment also included an evaluation of Panicum hemitomom establishment techniques with the intention of identifying means for streamlining the restoration process. For example, two treatments were completely hydroponic in that they lacked substrate and mat or containment materials, and two additional treatments received humic acid amendment as a means for enhancing Panicum hemitomom growth. Humic acid, a blend of plant-derived organic acids that is inexpensive and easily applied, has been shown to increase the growth and yield of agricultural crops (McAllister 1987; Chen and Aviad 1990). Evidence also exists suggesting that stem growth and reproductive output of Panicum amarum Ell., a common dune grass of the southeastern United States, can be enhanced with humic acid amendment (Willis and Hester, in press). One additional treatment tested a semi-impenetrable canvas underpinning fastened to the underside of a peat and Duralast coconut fiber mat. I hypothesized that the underpinning would result in a denser, more structurally-sound and well-integrated, root mat by way of root tactile stimulation and directional impedance.

This experiment represents one of the most detailed assessments of thick-mat floating marsh creation to date because it combined key findings from earlier experiments, notably those associated substrate and mat or containment materials, with avenues for enhancing overall creation success, specifically a multi-species approach and different Panicum hemitomom establishment techniques.

The objectives of this study were to:

- (1) Elucidate the influence of additional plant species on Panicum hemitomom growth response and patterns of biomass allocation within a floating marsh restoration context.
- (2) Determine the potential benefit of including additional plant species, particularly laterally-growing specialists, on floating marsh vegetative development.

Overarching hypothesis:

Panicum hemitomom growth response, patterns of biomass allocation, and overall created floating marsh vegetative development, will vary significantly according to multi-species combination and Panicum hemitomom establishment technique.

Key hypotheses:

1. In addition to being more species rich, created mats that include Panicum hemitomom and one or more accompanying secondary species will exhibit:
 - A. Greater vegetative cover, or the proportion of total area vegetated
 - B. Greater mat total biomass
 - C. Less Panicum hemitomom shoot, rhizome, and root biomass
2. Laterally-growing edge specialists will differ significantly among one another with respect to their:
 - A. Ability to colonize both open-water habitat and unvegetated areas of created mats
 - B. Relative contributions to total cover, or the proportion of total area vegetated
 - C. Inherent root morphological attributes
3. Panicum hemitomom grown in peat with Duralast coconut fiber, and either humic acid amendment or a canvas underpinning, as compared to the Panicum hemitomom only treatment, will exhibit:
 - A. Greater vegetative cover, or the proportion of total area vegetated
 - B. Greater total biomass and partitions of total biomass
 - C. Greater total rhizome length

Materials and Methods

Experimental design

This experiment (Image 4.1, top panel) was initiated in April of 2006, and completed after five months of growth in September of 2006 [note that an earlier version (Image 4.1, bottom panel) was destroyed by Hurricane Katrina after the plant acclimation phase, but prior to data collection]. The experimental design involved 12 treatments, each replicated 4 times in a completely randomized fashion, for a total of 48 experimental units ($n = 48$). For descriptive purposes, the 12 treatments have been divided into 7 vegetative, or multi-species treatments, and 5 Panicum hemitomon establishment techniques. With respect to the multi-species approach, five wetland-adapted plant species that are common constituents of thick-mat floating marsh were included in the design (Image 4.2). These included Panicum hemitomon, the dominant macrophyte of thick-mat floating marsh, and four herbaceous species including: Alternanthera philoxeroides (Mart.), Hydrocotyle ranunculoides L. f., Ludwigia peploides (Kunth) Raven, and Sagittaria lancifolia L. Of these, Alternanthera philoxeroides, Hydrocotyle ranunculoides, and Ludwigia peploides were laterally-growing edge specialists. Sagittaria lancifolia is not a laterally-growing edge specialist, but it is common in thick-mat floating marsh, often exhibiting secondary dominance, and at times, co-dominance (Sasser et al. 1995a and 1995b). I chose these species predominantly because of their lateral growth forms (Sagittaria lancifolia excluded), but also because they tend to be associated with marsh edges, and to a lesser extent, with open-water habitats. Whether these species are representative of different functional groups was not a deciding factor in their selection, although their explicitly different growth forms, compared to Panicum hemitomon, may be interpreted as having different functional implications for this research.



Image 4.1. Image showing the multi-species experiment after two months of growth (top image), and the initial attempt at conducting this experiment after being destroyed by Hurricane Katrina in August of 2005 (bottom image).

The 7 multi-species treatments, which included as few as one, and as many as five species, were as follows (including their respective treatment abbreviation): Panicum hemitomom only (Ph), Panicum hemitomom with Alternanthera philoxeroides (PhAp), Panicum hemitomom with Hydrocotyle ranunculoides (PhHr), Panicum hemitomom with Ludwigia peploides (PhLp), Panicum hemitomom with Sagittaria lancifolia (PhSl), Panicum hemitomom with all edge species, Sagittaria lancifolia excluded (Ph edge), and Panicum hemitomom with all species, Sagittaria lancifolia included (Ph all).

The 5 Panicum hemitomom establishment techniques were as follows (including their respective treatment abbreviation): Panicum hemitomom in chicken wire (PC), Panicum hemitomom in chicken wire with humic acid amendment (PCH), Panicum hemitomom in Duralast coconut fiber with bagasse (PDB), Panicum hemitomom in Duralast coconut fiber with peat and canvas underpinning (PDC), Panicum hemitomom in Duralast coconut fiber with peat and humic acid amendment (PDH). The bagasse used in the PDB treatment came from the same lot of one year-old bagasse used in experiment – 1 (Chapter 3), obtained from Raceland Sugar Company, Raceland, LA.

In each of the 7 multi-species treatments, ground sphagnum peat moss (Waupaca Northwoods LLC., Waupaca, WI), referred to as peat hereafter, served as the substrate material, whereas duralast coconut fiber served as the mat or containment material, both based on earlier findings reported herein (Chapter 3). As in previous experiments, a 3 to 5 cm layer of peat was sandwiched between a 3 cm top and bottom layer of Duralast coconut fiber, although in this case created mats were significantly larger (0.9 m²) than in previous experiments.

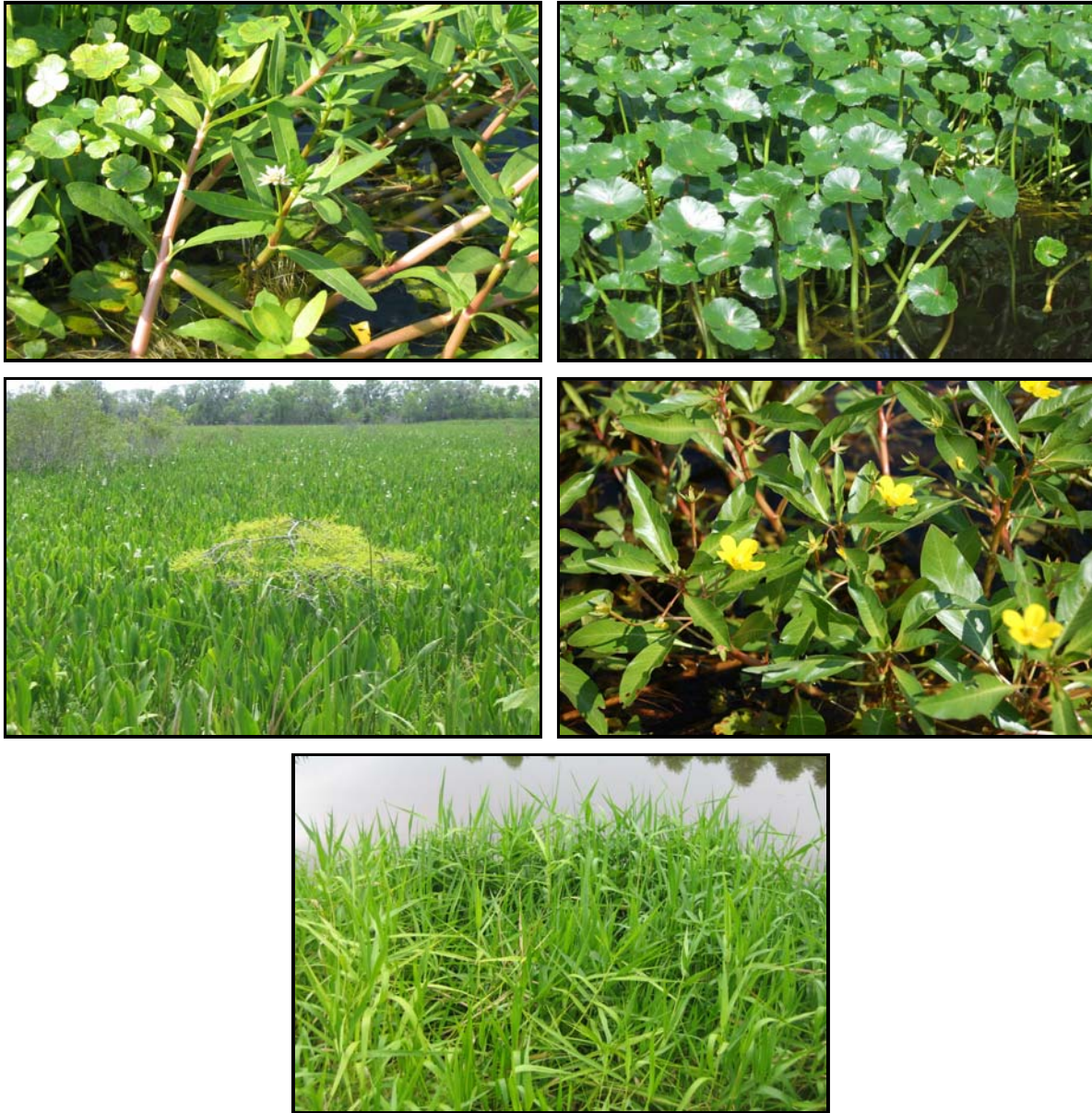


Image 4.2. Each of the plant species employed in the multi-species approach for enhancing floating marsh vegetative development (clockwise from the upper right). Hydrocotyle ranunculoides, a laterally-growing specialist; Ludwigia peploides, also a laterally-growing specialist; Panicum hemitomon, the dominant macrophyte of thick-mat floating marsh and the focal species of all restoration efforts; Sagittaria lancifolia, not a laterally-growing specialist but at times a thick-mat floating marsh co-dominant; Alternanthera philoxeroides, the third laterally-growing specialist.

All Panicum hemitomon plant material used in this experiment was harvested as root and rhizome stock from a single clone growing at the USDA Golden Meadow Plant Materials Center, Galliano, LA. Root and rhizome stock was transported back to the greenhouse facility at the University of New Orleans, and propagated for approximately six weeks in 10 cm plastic pots filled with enriched 18-6-12 (N-P-K respectively) Miracle-Gro potting soil (Scotts Miracle-Gro Company, Marysville, OH). Mesic hydrologic conditions were maintained for the entirety of the propagation period. All additional plant species, obtained from various freshwater wetlands, including road-side ditches and storm-water canals in Orleans, Jefferson, LaFourche, and St. John the Baptist Parishes, were transported back to the greenhouse facility at the University of New Orleans in water-filled plastic containers to minimize physiological stress and root desiccation. None of the additional plant species underwent propagation, rather all were planted in their respective treatments within 48 hours of being obtained.

All 12 treatments, regardless of species combination or establishment technique, received nine bare-root plugs of Panicum hemitomon, planted in a 3 x 3 arrangement. Panicum hemitomon plugs were approximately two months old at planting, and to avoid biased results, care was taken to ensure that initial Panicum hemitomon wet masses were uniform across all treatments. In treatments that received only one laterally-growing edge specialist, three bare-root plugs of that particular species were planted per side around the periphery of each created mat, totaling twelve laterally-growing edge-specialist plugs per mat. In those treatments that included all three laterally-growing edge specialists, one bare-root plug per species was planted per side around the periphery of each created mat, resulting in four plugs per species per mat (or 12 edge-specialist plugs total). In the treatment that included all possible species combinations, four bare-root plugs of Sagittaria lancifolia were planted in open locations within the nine Panicum hemitomon plugs, whereas all other secondary species were planted using the

same approach as used for the all edge-species treatment. Therefore, the all-species treatment had higher initial plant density than any other treatment.

All treatments were maintained in a fully-exposed outdoor setting at the University of New Orleans' greenhouse facility. Experimental vessels were 1330-L (2.6 m² surface area equivalent) livestock watering tanks filled to capacity with a combination of tap and rain water. Buoyancy for all twelve treatments was achieved using a square support structure fashioned from 3.8 cm diameter polyvinyl chloride (PVC) pipe. Each created mat (chicken wire treatments excluded) was supported within the flotation device by a cross-weaving of nylon rope (2 per side).

The fertilization regime was the same as with all previous experiments in that it was based on peak values in the range of mean annual nitrogen and phosphorous outflow loading rates (8.9 – 23.5 g N m⁻² yr⁻¹ and 0.9 – 2.0 g P m⁻² yr⁻¹ respectively) as reported by Lane et al. (1999) from the Caernarvon diversion, Caernarvon, LA. Slow release granular Osmocote fertilizer (Scotts Miracle-Gro Company, Marysville, OH) with a guaranteed analysis of 18-6-12 (N-P-K respectively) was applied monthly at an annual loading rate of 25 g N m⁻² yr⁻¹ and 2 g P m⁻² yr⁻¹. The humic acid amendment, 3.0% active ingredient Actisol (Arctec Inc, Little Rock, AR), was applied as a foliar spray at a rate of 4 ml m⁻² mo⁻¹ on the first of each month over the five-month course of the experiment.

Vegetative cover

At monthly intervals over the course of the experiment, digital images were taken using a Nikon D-50 SLR camera (Nikon Inc., Melville, NY) mounted on a constructed, portable tripod set at a height of approximately 2 m above each experimental unit. Each subsequent image of sufficient quality was digitally overlain by a uniformly-sized grid to enable the estimation of vegetative cover, and the proportion of total area vegetated by each species. Each cell was

viewed for vegetation presence or absence, and when cells contained more than one species, the dominant species was given preference. The dimensions of the grid were slightly larger than the vessel dimensions because it was assumed that the laterally-growing specialists would grow beyond the confines of the vessels. As a result, the proportion of total area vegetated never reached 1.0 in any treatment even though several tanks appeared fully vegetated.

Root data

Root specific gravity was assessed for each species using five live root samples per species, all sampled from the Panicum hemitomon with all-species treatment. This was done to ensure uniform treatment conditions for all samples. A representative sample of twenty roots per species was obtained from the Panicum hemitomon with all species treatment (five from each of the four vessels), and assigned a unique ID. A random number generator was used to select five roots per species for analyses. As with previous experiments, root specific gravity was determined using between 0.05 and 0.10 g of freshly-harvested tissue, and the pycnometer method as described by Burdick (1989). Root specific gravity (RSG) was computed using the formula: $RSG = R / (P + R - PR)$, where R = mass of roots, P = mass of water-filled pycnometer, and PR = mass of pycnometer with roots and water.

In this experiment, root morphometrics refer to attributes of a single root as opposed to attributes of an entire root system. Root morphometrics included root length, diameter, volume, and number of root tips. All root morphometrics were assessed by first digitizing roots using an Epson 10000-XL scanner, and second by analyzing each digital image using WinRhizo Pro-version Root Imaging Software (Regent Instruments, Québec, Canada). As with root specific gravity, five live root samples per species were obtained from the Panicum hemitomon with all-species treatment using the same selection methodology, but a different lot of roots.

Biomass harvest

Total mat biomass was determined by completely censusing each created mat (Image 4.3). All harvested biomass was sorted by species, but the partitioning of biomass into above- and belowground components occurred only for Panicum hemitomon. Biomass for each additional species was not partitioned into specific components because of temporal constraints and morphologically different growth forms, but rather lumped into a total biomass metric. Panicum hemitomon aboveground biomass was defined as all shoot biomass emerging from the top and underside of each vegetated mat. The surface of the water served as the clipping benchmark for all rhizomes with emerging stems. All rhizome material below the first node from which roots were visible was considered belowground biomass. All visible root and rhizome material was clipped from the bottom of each vegetated mat, and all root and rhizome material that became incorporated within each mat was recovered by first disassembling each mat and extracting all visible biomass, and second by thoroughly rinsing all substrate material with water and passing it through a 1.5 mm sieve. This also ensured the recovery of all fine root material. The length of all Panicum hemitomon rhizome material was measured before drying to determine the total rhizome length. As previously noted (Chapter 2), rhizome length served as a surrogate for lateral spreading potential, as Panicum hemitomon is predominantly a clonal species.

All biomass was placed in labeled paper bags and oven-dried at 60°C for approximately ten days, or until a constant mass was attained. Although rhizome material was dried separately to provide a measure independent of root material, when reference is made to total belowground biomass or belowground production, the two were summed.

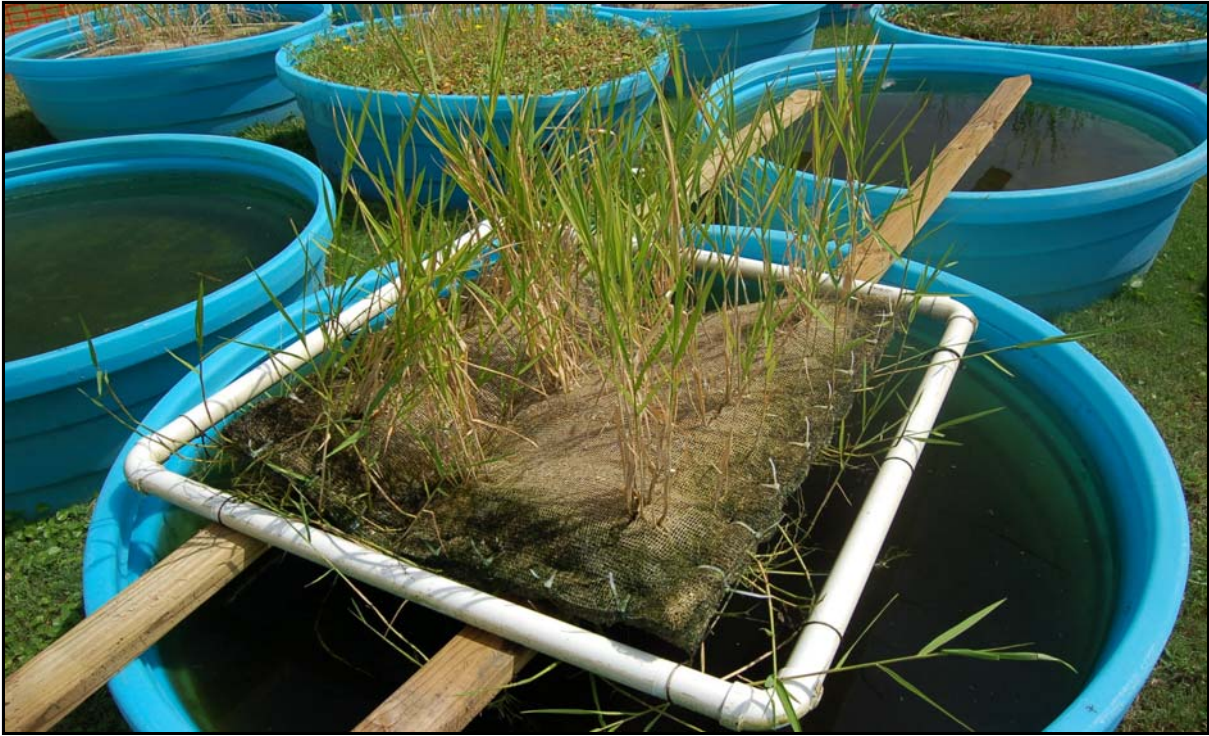


Image 4.3. Image of vegetated mat at harvest prior to clipping shoot (top image) and rhizome and root biomass (bottom image).

Panicum hemitomom root volume was estimated for each created mat using the root dry mass obtained in this experiment, and a root volumetric multiplier derived from a total census of root volume in a different experiment, the phase – II study (Chapter 2). Note that treatments with similar nutrient regime ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $5 \text{ g P m}^{-2} \text{ yr}^{-1}$), and a comparable hydrologic regime (saturated hydrologic conditions), were used in deriving this metric.

Statistical analyses

SAS Version 9.1 (SAS Institute, Cary, NC) was used for all statistical analyses reported herein. All variables were evaluated independently to ensure that each clearly met the normality and heteroscedasticity assumptions associated with analysis of variance (ANOVA). A two-way ANOVA using the SAS PROC GLM procedure was used to test for differences in all non-sequentially measured variables, where as a multivariate repeated measures analysis of variance (MANOVA), also using the SAS PROC GLM procedure, was used to test for significant differences in sequentially measured variables. A significance level of $\alpha = 0.05$ was used for all statistical tests unless specified otherwise. For MANOVA tests, preference was given to Wilk's lambda when test of significance values did not differ. When differences existed, Pillai's trace was chosen because of its robustness to violations of assumptions (Kleinbaum et al. 1998; Scheiner and Gurevitch 2001). Post-hoc statistical tests were performed when considered ecologically significant, such as on the final round of sequentially-sampled variables. Other post-hoc tests, when performed, are reported in the Appendix.

The Panicum hemitomom only treatment has been included in analyses of establishment technique for comparative purposes because it represents the baseline treatment, or treatment to which all other treatments were relative. It is also the treatment that would be recommended for restoration use if no other treatment, establishment technique or multi-species combination, proved to be vegetatively superior.

Results

Vegetative cover

Panicum hemitomon total vegetative cover for establishment technique (Figure 4.1; Image 4.4), measured as the proportion of total area vegetated, increased significantly for half of the treatments over the course of the experiment (Wilk's Lambda: $F_{2,17} = 62.03$, $p < 0.0001$), the exceptions being the two hydroponic treatments (PC and PCH), and the treatment that employed bagasse as a substrate (PDB). The rate at which vegetative cover increased, and to a lesser extent decreased, also varied significantly (Pillai's Trace: $F_{10,36} = 6.27$, $p < 0.0001$). The three establishment techniques for which Panicum hemitomon vegetative cover increased over time (PD, PDC, and PDH), were not statistically significant from another at harvest in September.

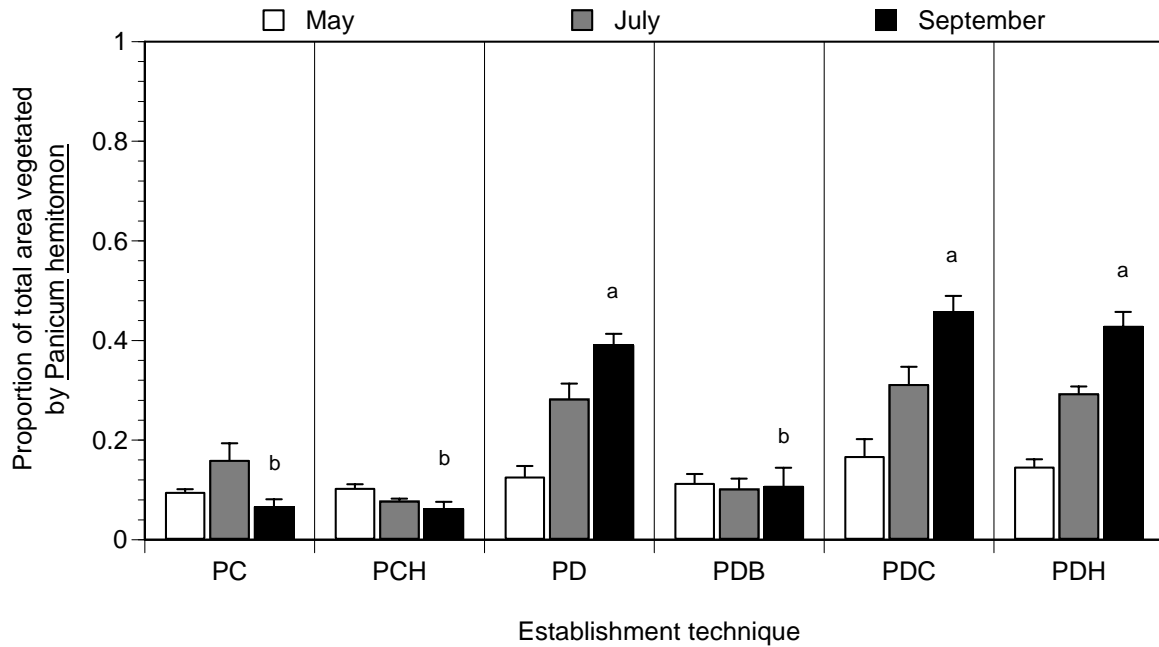


Figure 4.1. The effect of establishment technique on the proportion of total area vegetated by Panicum hemitomon, measured monthly over a five-month period. Treatment codes are as follows: PC = Panicum hemitomon in chicken wire; PCH = Panicum hemitomon in chicken wire with humic acid amendment; PD = Panicum hemitomon in Duralast coconut fiber with peat; PDB = Panicum hemitomon in Duralast coconut fiber with bagasse; PDC = Panicum hemitomon in Duralast coconut fiber with peat and canvas underpinning; PDH = Panicum hemitomon in Duralast coconut fiber with peat and humic acid amendment. Values are means \pm SE ($n = 4$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for September data only ($F_{5,18} = 56.94$, $p < 0.0001$).



Image 4.4. Images of three *Panicum hemitomon* establishment techniques. *Panicum hemitomon* in Duralast coconut fiber with peat (PD treatment), the baseline treatment (top image); *Panicum hemitomon* in Duralast coconut fiber with peat and canvas underpinning (PDC treatment), the best-performing establishment technique (middle image); *Panicum hemitomon* in chicken wire (PC treatment), the worst-performing establishment technique (bottom image).

The proportion of total area vegetated for all multi-species treatments (Figure 4.2; Image 4.5), which incorporated vegetative cover for Panicum hemitomom and each secondary species when present, increased in all treatments over the course of the experiment (Wilk's Lambda: $F_{2,20} = 149.87$, $p < 0.0001$). The exceptions were the Panicum hemitomom with Ludwigia peploides and the Panicum hemitomom with all species treatments, which did not increase substantially after the July sampling because of an insect-induced defoliation event between the July and August samplings. The rate of increase in the proportion of total area vegetated differed significantly according to species combination (Pillai's Trace: $F_{12,42} = 4.74$, $p < 0.0001$), with the greatest increase exhibited by treatments containing Ludwigia peploides (at least up until the defoliation event occurred). Interestingly, the greatest vegetative cover, or proportion of total area vegetated, was attained not by the treatment with the greatest number of species (and greatest density of planting units), but by a two-species combination. Vegetative cover for the Panicum hemitomom with Ludwigia peploides treatment reached 0.70, which was greater than any other species combination. The Panicum hemitomom with Hydrocotyle ranunculoides and Panicum hemitomom with Sagittaria lancifolia treatments both attained significantly less vegetative cover (0.36 and 0.38 respectively), which as evidenced by the September cover data, did not differ significantly from the Panicum hemitomom only treatment.

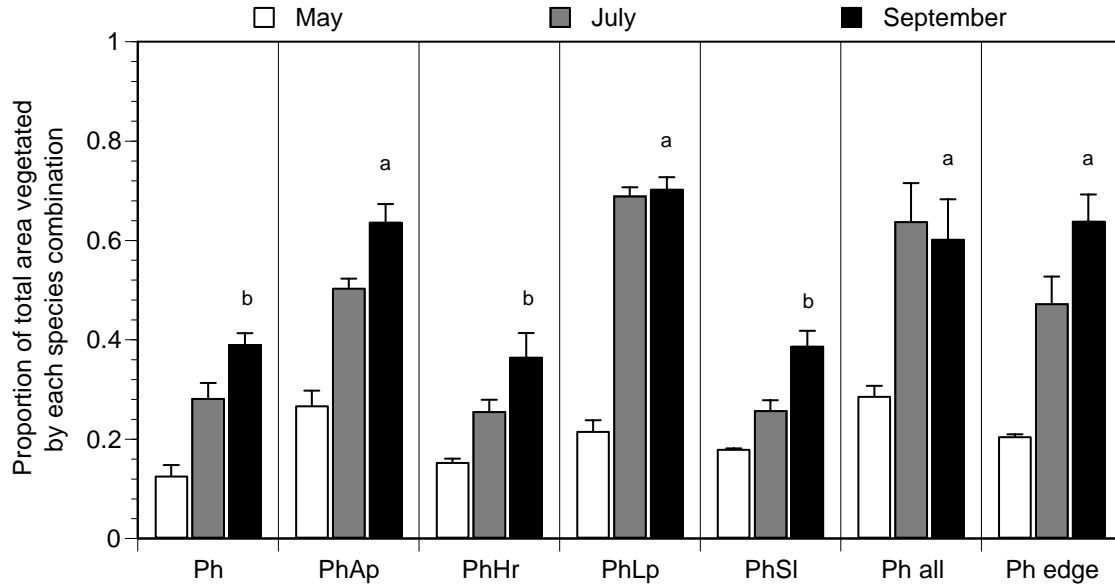


Figure 4.2. The effect of multi-species combination on the proportion of total area vegetated, measured monthly over a five-month period. Treatment codes are as follows: Ph = Panicum hemitomom only; PhAp = Panicum hemitomom with Alternanthera philoxeroides; PhHr = Panicum hemitomom with Hydrocotyle ranunculoides; PhLp = Panicum hemitomom with Ludwigia peploides; PhSl = Panicum hemitomom with Sagittaria lancifolia; Ph all = Panicum hemitomom with all species (including Sagittaria lancifolia); Ph edge = Panicum hemitomom with all edge species (excluding Sagittaria lancifolia). Values are means \pm SE ($n = 4$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for September data only ($F_{6,21} = 9.99$, $p < 0.0001$).

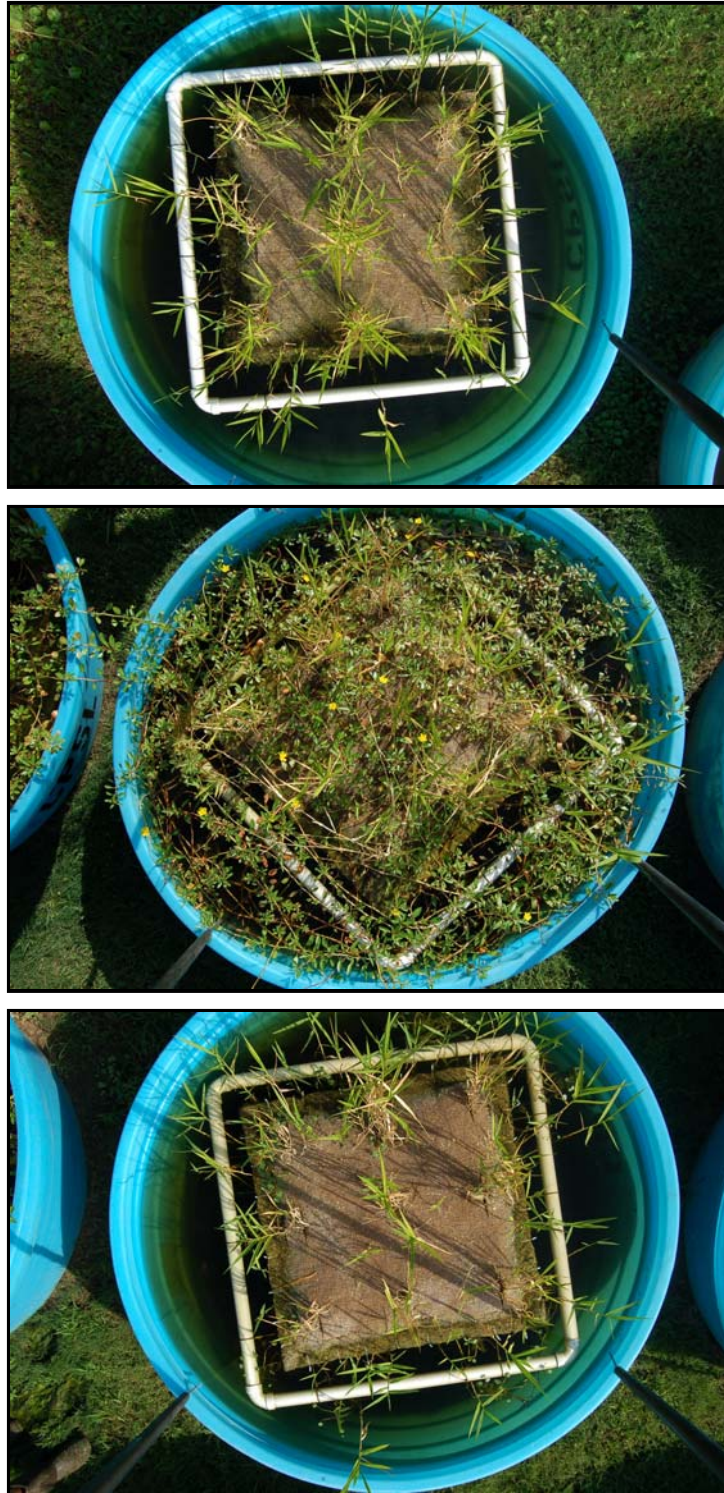


Image 4.5. Images of three multi-species treatments. Panicum hemitomon only, the baseline treatment (top image); Panicum hemitomon with Ludwigia peploides, the best-performing multi-species treatment but post-defoliation event (middle image); Panicum hemitomon with Hydrocotyle ranunculoides, the worst-performing multi-species treatment (bottom image).

The proportion of total area vegetated by Panicum hemitomom for each multi-species combination (Figure 4.3) varied significantly across treatments ($F_{6,21} = 18.68$, $p < 0.0001$), with the Panicum hemitomom only treatment exhibiting the greatest proportional contribution, or in this case, total contribution. With respect to the Panicum hemitomom contribution in other treatments, generally speaking, the more vigorously the secondary species grew, the less was the contribution of Panicum hemitomom to the proportion of total area vegetated.

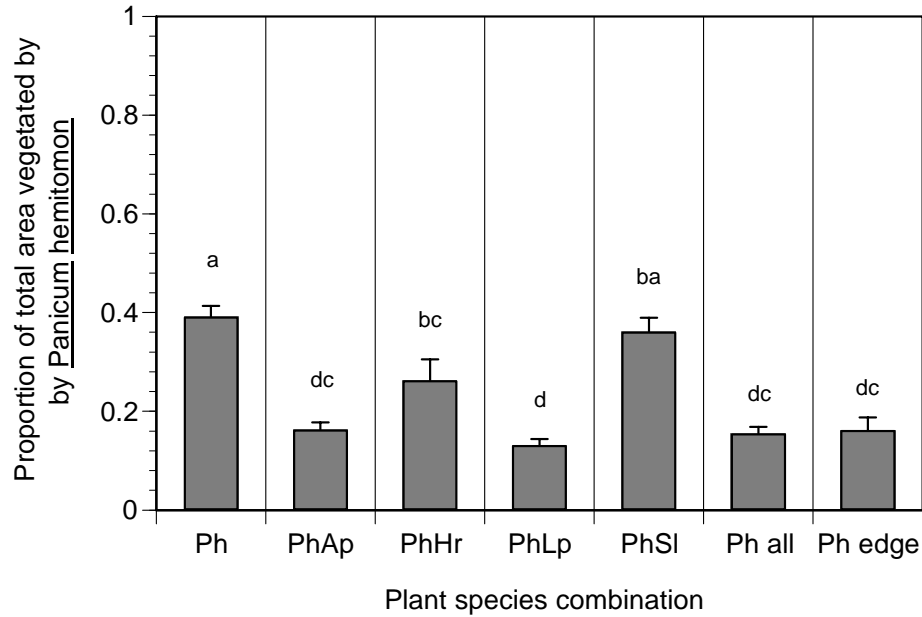


Figure 4.3. The effect of multi-species combination on the proportion of total area vegetated by *Panicum hemitomon*, determined at harvest. Treatment codes are as follows: Ph = *Panicum hemitomon* only; PhAp = *Panicum hemitomon* with *Alternanthera philoxeroides*; PhHr = *Panicum hemitomon* with *Hydrocotyle ranunculoides*; PhLp = *Panicum hemitomon* with *Ludwigia peploides*; PhSl = *Panicum hemitomon* with *Sagittaria lancifolia*; Ph all = *Panicum hemitomon* with all species (including *Sagittaria lancifolia*); Ph edge = *Panicum hemitomon* with all edge species (excluding *Sagittaria lancifolia*). Values are means \pm SE ($n = 4$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{6,21} = 18.68$, $p < 0.0001$).

When Panicum hemitomom and each secondary species in two-species combinations were evaluated individually (Figure 4.4), mixed results were observed with respect to which of the two species contributed more to the proportion of total area vegetated. For the Panicum hemitomom with Ludwigia peploides treatment, there were significant increases in vegetative cover over the course of the experiment (Wilk's Lambda: $F_{2,5} = 227.81$, $p < 0.0001$), as well as a highly significant difference in the rate at which these species contributed to the proportion of total area vegetated (Wilk's Lambda: $F_{2,5} = 164.64$, $p < 0.0001$). Similar statistical results were observed for the Panicum hemitomom with Alternanthera philoxeroides treatment with respect to vegetative cover (Wilk's Lambda: $F_{2,5} = 25.40$, $p = 0.0024$), and for the rate at which these species contributed to the proportion of total area vegetated (Wilk's Lambda: $F_{2,5} = 9.70$, $p = 0.0190$). For the Panicum hemitomom with Ludwigia peploides and the Panicum hemitomom with Alternanthera philoxeroides treatments, the secondary species, not Panicum hemitomom, contributed more to the proportion of total area vegetated. For the Panicum hemitomom with Hydrocotyle ranunculoides treatment, a significant increase in vegetative cover was observed over the course of the experiment (Wilk's Lambda: $F_{2,5} = 15.20$, $p = 0.0075$), but it was almost exclusively Panicum hemitomom contributing to increased in cover. The rate at which Panicum hemitomom contributed to total vegetative cover was therefore significantly greater (Wilk's Lambda: $F_{2,5} = 9.34$, $p = 0.0205$). For the Panicum hemitomom with Sagittaria lancifolia treatment, vegetative cover varied significantly over the course of the experiment (Wilk's Lambda: $F_{2,5} = 23.01$, $p = 0.0030$), with Panicum hemitomom cover increasing and Sagittaria lancifolia cover decreasing. As a result, the rate of increase (and decrease) for this treatment was significant (Wilk's Lambda: $F_{2,5} = 44.05$, $p = 0.0007$).

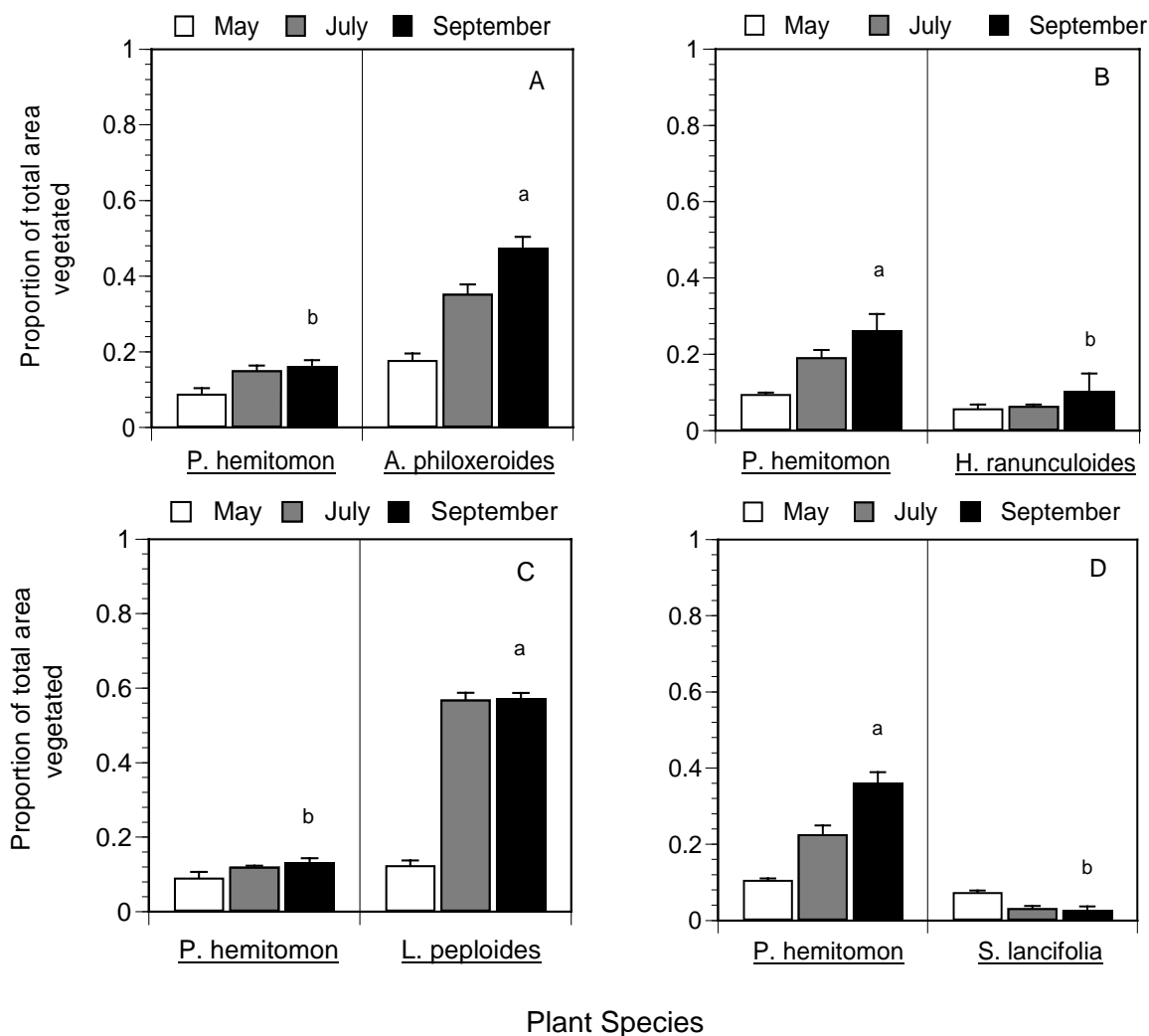


Figure 4.4. Individual species contributions to the proportion of total area vegetated for each two-species combination, measured monthly over a five-month period. Figure codes are as follows: A = *Panicum hemitomon* with *Alternanthera philoxeroides*; B = *Panicum hemitomon* with *Hydrocotyle ranunculoides*; C = *Panicum hemitomon* with *Ludwigia peploides*; D = *Panicum hemitomon* with *Sagittaria lancifolia*. Values are means \pm SE ($n = 4$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for September data only (A: $F_{1,6} = 88.56$, $p < 0.0001$), (B: $F_{1,6} = 6.42$, $p = 0.0444$), (C: $F_{1,6} = 553.22$, $p < 0.0001$), (D: $F_{1,6} = 125.86$, $p < 0.0001$).

As expected based on results observed for two-species combinations, vegetative cover for species combinations with more than two species also exhibited significant species effects. The Panicum hemitomom with all edge-species treatment (Figure 4.5, top panel), exhibited a significant increase in vegetative cover over the course of the experiment (Wilk's Lambda: $F_{2,11} = 6.97$, $p = 0.0111$), with Ludwigia peploides, and to a lesser extent, Panicum hemitomom, contributing the most to the proportion of total area vegetated. A significant difference for the rate at which these species contributed to vegetative cover was also observed (Pillai's Trace: $F_{8,24} = 5.26$, $p = 0.0007$).

Similar results were observed for the Panicum hemitomom with all species treatment (Figure 4.5, bottom panel). Vegetative cover increased significantly over the course of the experiment (Wilk's Lambda: $F_{2,14} = 5.83$, $p = 0.0144$), with Ludwigia peploides, and to a lesser extent, Panicum hemitomom, contributing the greatest. The rate at which these species contributed to total vegetative cover also varied significantly (Pillai's Trace: $F_{8,30} = 2.35$, $p = 0.0433$). In both of these treatments, Ludwigia peploides was identified as the dominant species because it contributed the greatest to mat vegetative cover.

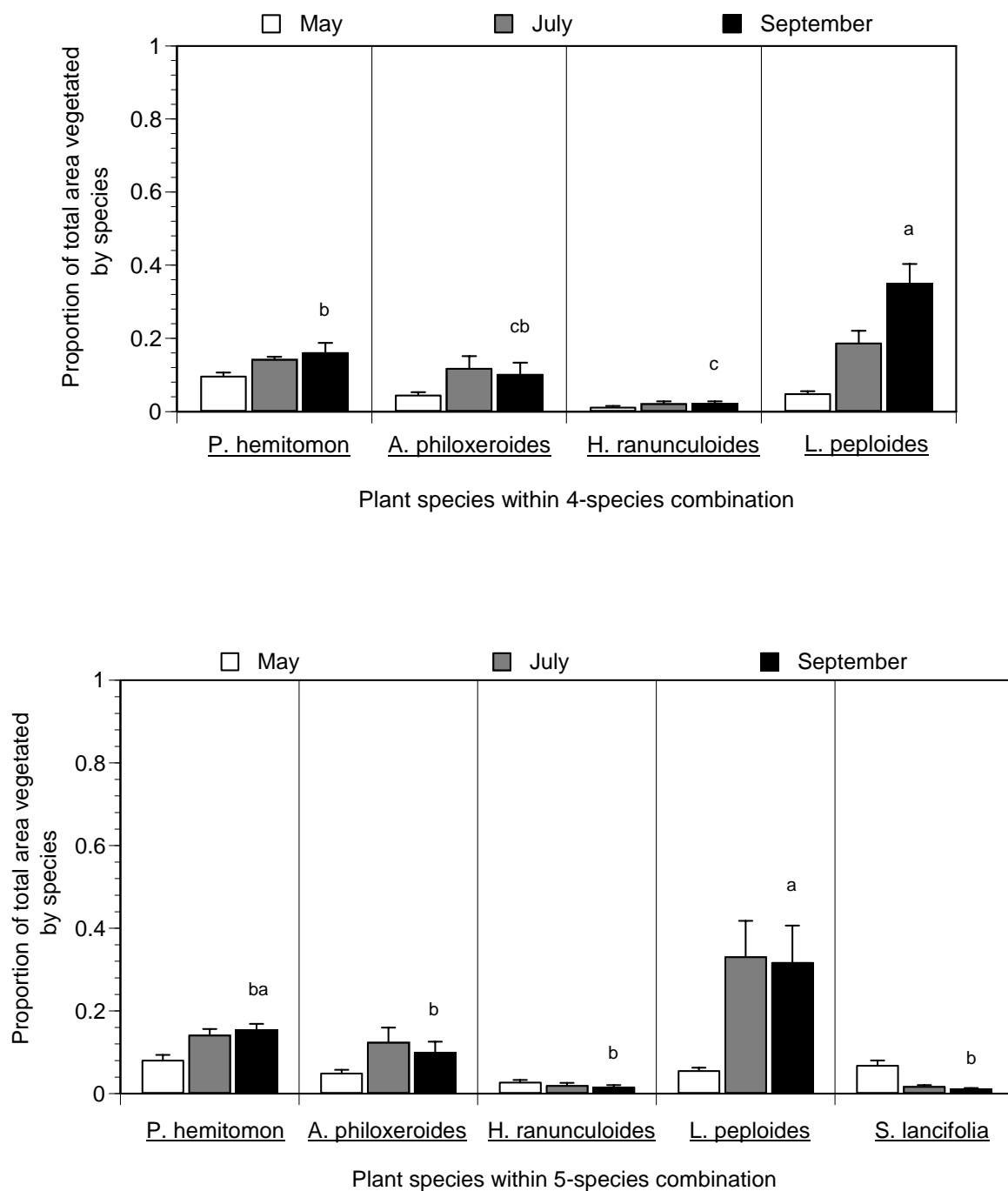


Figure 4.5. The effect of plant species combination on the proportion of total area vegetated by each species, measured monthly over a five-month period. Shown are the Ph edge treatment (top panel) and the Ph all treatment (bottom panel). Values are means \pm SE ($n = 4$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$) for September data only (top panel: $F_{3,12} = 18.07$, $p < 0.0001$) and (bottom panel: $F_{4,15} = 9.17$, $p = 0.0006$).

Root data

Root specific gravity (Figure 4.6) varied significantly across species ($F_{5,24} = 191.60$, $p \leq 0.0001$). Ludwigia peploides roots exhibited the lowest root specific gravity (0.12), whereas Alternanthera philoxeroides roots exhibited the greatest (0.99), and consequently were the least buoyant. Interestingly, Ludwigia peploides produces two types of roots, downward and upward-growing roots. Unlike their upward-growing counterparts, which were highly buoyant (0.12), downward-growing roots were much less so (0.87), but still buoyant. Hydrocotyle ranunculoides root specific gravity (0.96) was similar to that of Alternanthera philoxeroides, whereas Panicum hemitomon and Sagittaria lancifolia roots exhibited similar, but lower root specific gravity (0.68 and 0.65 respectively).

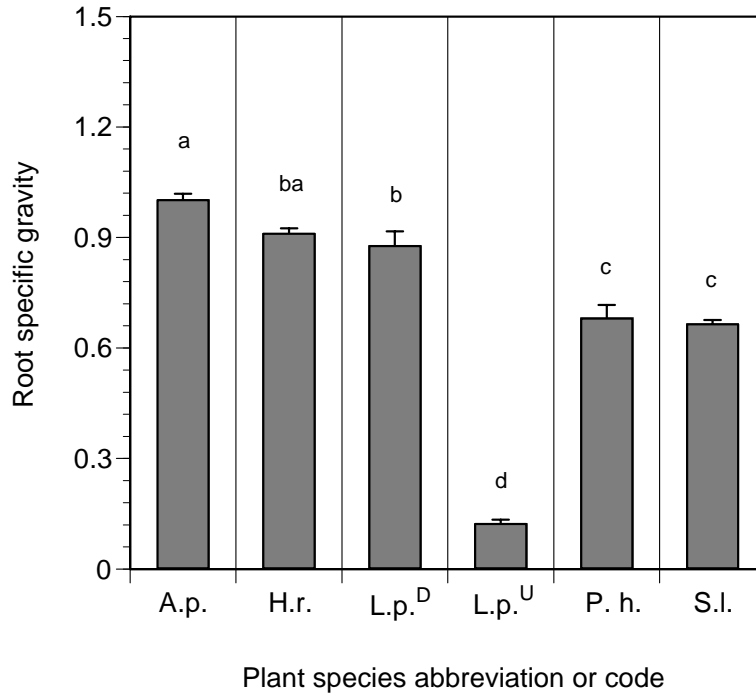


Figure 4.6. Root specific gravity of each species included in the multi-species planting approach, all measured on live root tissue sampled from the Panicum hemitomom with all species treatment. Treatment codes are as follows: P.h. = Panicum hemitomom; A.p. = Alternanthera philoxeroides; H.r. = Hydrocotyle ranunculoides; L.p.^D = Ludwigia peploides downward-growing root; L.p.^U = Ludwigia peploides upward-growing root; S.l. = Sagittaria lancifolia. Values are means \pm SE (n = 5). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{5,24} = 191.60$, $p < 0.0001$).

Root morphological metrics varied widely across species (Table 4.1). A highly significant species effect was observed for mean root length ($F_{4,15} = 20.97$, $p < 0.0001$), with downward-growing Ludwigia peploides roots exhibiting the greatest length, not necessarily because of the overall length of the tap root, but due to their herringbone morphology and the exorbitant number of first-order lateral roots. Roots of Panicum hemitomom had fewer lateral roots, and were consequently shorter in total length, although still longer than each of the other species. A highly significant difference was also observed for mean root diameter ($F_{4,15} = 10.93$, $p = 0.0002$), with Panicum hemitomom exhibiting greater mean root diameter than each of the secondary species. Root volume also varied significantly across species ($F_{4,15} = 11.20$, $p = 0.0002$). The greatest mean root volume was exhibited by Ludwigia peploides, and although less, Panicum hemitomom root volume was still greater than each of the other secondary species. Much like root length and diameter, the number of root tips varied significantly as well ($F_{4,15} = 4.39$, $p = 0.0151$), with Ludwigia peploides exhibiting the greatest mean number of root tips, again attributable to their herringbone morphology. Importantly, Ludwigia peploides roots had a greater number of first-order lateral roots, whereas Panicum hemitomom roots branched more extensively beyond the first-order division, a trait indicative of grasses and fibrous root systems.

Table 4.1. Mean root diameter (mm), length (cm), volume (cm³), and number of root tips for each of the five plant species used to assess multi-species effects on floating marsh vegetative development. Values are means \pm SE (n = 5).

Species	Diameter (mm)	Length (cm)
<u>Alternanthera philoxeroides</u>	0.18 \pm 0.004 ^c	54.7 \pm 8.44 ^b
<u>Hydrocotyle ranunculoides</u>	0.39 \pm 0.029 ^{bc}	18.7 \pm 0.50 ^b
<u>Ludwigia peploides</u>	0.32 \pm 0.022 ^{bc}	535.7 \pm 85.4 ^a
<u>Panicum hemitomon</u>	0.62 \pm 0.105 ^a	153.5 \pm 61.7 ^b
<u>Sagittaria lancifolia</u>	0.54 \pm 0.035 ^{ba}	35.2 \pm 2.69 ^b
<i>F</i> – value (df4,15)	10.93 ^{**}	20.97 ^{**}
Species	Volume (cm ³)	Number of tips
<u>Alternanthera philoxeroides</u>	0.01 \pm 0.001 ^b	117.7 \pm 11.77 ^b
<u>Hydrocotyle ranunculoides</u>	0.02 \pm 0.004 ^b	7.75 \pm 4.46 ^b
<u>Ludwigia peploides</u>	0.61 \pm 0.0.16 ^a	1972.2 \pm 871.65 ^a
<u>Panicum hemitomon</u>	0.34 \pm 0.058 ^{ba}	299.7 \pm 147.44 ^b
<u>Sagittaria lancifolia</u>	0.07 \pm 0.006 ^b	112.2 \pm 4.95 ^b
<i>F</i> – value (df 4,15)	11.20 ^{**}	4.39 [*]

^a Means with same letter in same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference ($p < 0.01$); ^{*} significant difference ($p < 0.05$).

Biomass harvest

Panicum hemitomom total biomass for each multi-species treatment was partitioned into shoot, rhizome, and root components to allow for component-specific analyses (Table 4.2 and Figure 4.7). Shoot biomass, ranging only from 78.7 g (Ph all treatment) to 111.7 g (Ph treatment), did not vary significantly with respect to multi-species treatment. In contrast, Panicum hemitomom rhizome biomass did exhibit a significant treatment effect ($F_{6,21} = 3.19$, $p = 0.0219$), ranging from 55.9 g (PhLp treatment) to 101.9 g (Ph treatment). An interesting finding with respect to these data was that Panicum hemitomom rhizome biomass, but not root biomass, was less for the Panicum hemitomom with Ludwigia peploides treatment than for the Panicum hemitomom only treatment. This suggests that Ludwigia peploides belowground production had a greater competitive effect on Panicum hemitomom rhizome growth than it did on root growth. This is further supported by data partitions of Panicum hemitomom biomass viewed on a proportional basis (Appendix, Table 13). Similar to that of shoot biomass, Panicum hemitomom root biomass did not vary significantly across treatment ($F_{6,21} = 0.29$, $p = 0.9331$), ranging only from 78.1 g (PhHr treatment) to 97.1 g (PhSl treatment). Panicum hemitomom total biomass, ranging from 231.8 g (PhLp treatment) to 300.9 g (Ph treatment), did not vary significantly according to multi-species treatment either, although totals were greater for the Panicum hemitomom only treatment.

Table 4.2. *Panicum hemitomom* total biomass (g), partitioned by component (shoot, rhizome, and root contributions) for each multi-species treatment. Treatment codes are as follows: Ph = *Panicum hemitomom* only; PhAp = *Panicum hemitomom* with *Alternanthera philoxeroides*; PhHr = *Panicum hemitomom* with *Hydrocotyle ranunculoides*; PhLp = *Panicum hemitomom* with *Ludwigia peploides*; PhSl = *Panicum hemitomom* with *Sagittaria lancifolia*; Ph all = *Panicum hemitomom* with all species; Ph edge = *Panicum hemitomom* with all species except *Sagittaria lancifolia*. Values are means \pm SE (n = 4).

Treatment	Shoot biomass (g)	Rhizome biomass (g)	Root biomass (g)	Total biomass (g)
Ph	111.7 \pm 11.4 ^a	101.9 \pm 9.0 ^a	87.3 \pm 17.3 ^a	300.9 \pm 37.4 ^a
PhAp	90.5 \pm 15.4 ^a	78.6 \pm 16.6 ^{ba}	94.5 \pm 16.3 ^a	263.8 \pm 95.3 ^a
PhHr	83.2 \pm 7.0 ^a	71.5 \pm 6.9 ^{ba}	78.1 \pm 6.6 ^a	232.9 \pm 38.7 ^a
PhLp	88.3 \pm 1.9 ^a	55.9 \pm 3.22 ^{ba}	87.5 \pm 4.5 ^a	231.8 \pm 17.2 ^a
PhSl	90.4 \pm 4.9 ^a	92.7 \pm 8.6 ^{ba}	97.1 \pm 15.6 ^a	280.3 \pm 48.1 ^a
Ph all	78.7 \pm 7.2 ^a	67.3 \pm 5.1 ^{ba}	84.8 \pm 5.6 ^a	230.96 \pm 22.7 ^a
Ph edge	88.6 \pm 9.1 ^a	79.5 \pm 2.1 ^b	90.8 \pm 6.5 ^a	259.0 \pm 33.6 ^a
<i>F</i> – value (df 6,21)	1.29 ^{NS}	3.19 [*]	0.29 ^{NS}	1.27 ^{NS}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{*} Significant difference ($p < 0.05$); ^{NS} non-significant difference ($p > 0.05$).

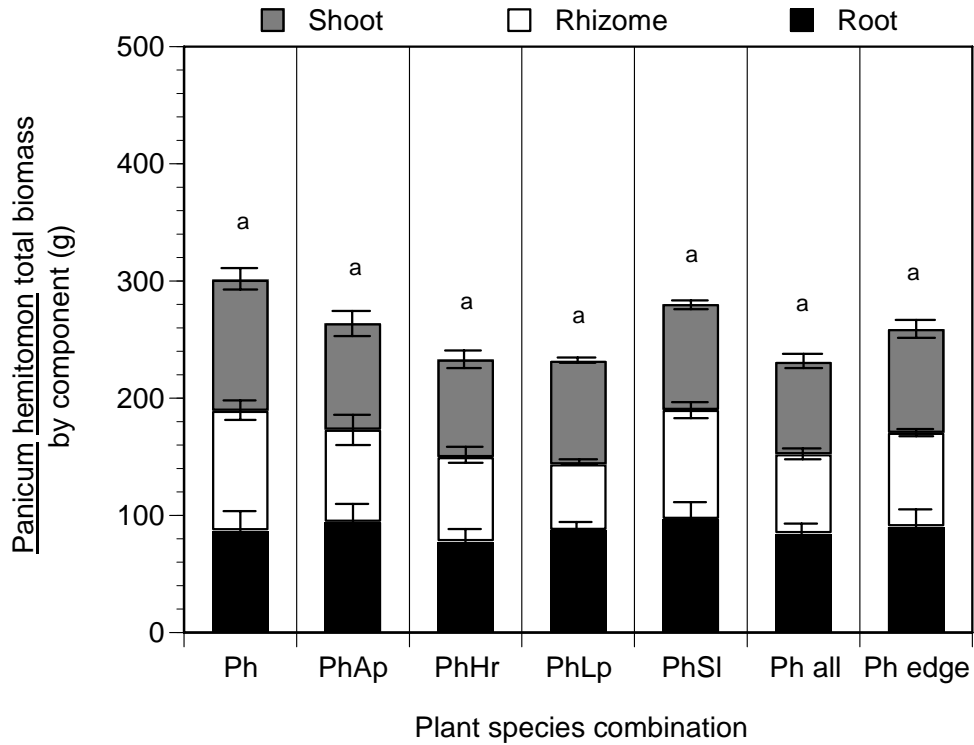


Figure 4.7. The effect of multi-species combination on *Panicum hemitomon* total biomass (g) partitioned by component (shoot, rhizome, and root). Treatment codes are as follows: Ph = *Panicum hemitomon* only; PhAp = *Panicum hemitomon* with *Alternanthera philoxeroides*; PhHr = *Panicum hemitomon* with *Hydrocotyle ranunculoides*; PhLp = *Panicum hemitomon* with *Ludwigia peploides*; PhSl = *Panicum hemitomon* with *Sagittaria lancifolia*; Ph all = *Panicum hemitomon* with all species (including *Sagittaria lancifolia*); Ph edge = *Panicum hemitomon* with all edge species (excluding *Sagittaria lancifolia*). Values are means \pm SE ($n = 4$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{6,21} = 1.27$, $p = 0.3137$).

As with the multi-species treatments, Panicum hemitomon total biomass for each establishment technique was separated into shoot, rhizome, and root components to allow for component-specific analyses (Table 4.3 and Figure 4.8).

Panicum hemitomon shoot biomass varied significantly according to establishment technique ($F_{5,18} = 22.03$, $p < 0.0001$), ranging from 20.2 g (PCH treatment) to 152.3 g (PDC treatment). Rhizome biomass also varied significantly ($F_{5,18} = 42.58$, $p < 0.0001$), ranging from 9.1 g (PCH treatment) to 118.7 g (PDH treatment). Similarly, Panicum hemitomon root biomass exhibited a highly significant treatment effect ($F_{5,18} = 15.39$, $p < 0.0001$), ranging from 20.4 g (PCH treatment) to 122.3 g (PDC treatment). As would be expected based on statistically-significant component-specific analyses, Panicum hemitomon total biomass varied significantly according to establishment technique ($F_{5,18} = 33.55$, $p < 0.0001$), ranging from 49.8 g (PCH treatment) to 376.3 g (PDH treatment). Significant differences were not observed for any partition of Panicum hemitomon biomass among the three best-performing techniques, although for these treatments (PDC, PDH, and PD respectively), shoot (and root) biomass tended to be greater for the PDC treatment, whereas rhizome biomass tended to be greater for the PDH treatment.

Table 4.3. Panicum hemitomom total biomass (g) partitioned by component (shoot, rhizome, and root contributions) for each establishment technique. Treatment codes are as follows: PC = Panicum hemitomom in chicken wire; PCH = Panicum hemitomom in chicken wire with humic acid amendment; PD = Panicum hemitomom in Duralast coconut fiber with peat; PDB = Panicum hemitomom in Duralast coconut fiber with bagasse; PDC = Panicum hemitomom in Duralast coconut fiber with peat and canvas underpinning; PDH = Panicum hemitomom in Duralast coconut fiber with peat and humic acid amendment. Values are means \pm SE (n = 4).

Treatment	Shoot biomass (g)	Rhizome biomass (g)	Root biomass (g)	Total biomass (g)
PC	23.2 \pm 5.58 ^b	12.8 \pm 2.6 ^b	20.7 \pm 5.1 ^b	56.8 \pm 26.37 ^a
PCH	20.2 \pm 4.54 ^b	9.1 \pm 1.9 ^b	20.4 \pm 4.2 ^b	49.8 \pm 21.17 ^a
PD	111.7 \pm 11.4 ^a	101.9 \pm 9.02 ^a	87.3 \pm 17.3 ^a	300.9 \pm 37.46 ^b
PDB	28.6 \pm 6.0 ^b	22.4 \pm 8.8 ^{ba}	32.0 \pm 12.6 ^b	83.1 \pm 54.25 ^a
PDC	152.3 \pm 25.5 ^a	101.6 \pm 13.4 ^a	122.3 \pm 12.6 ^a	376.3 \pm 98.79 ^b
PDH	123.1 \pm 9.0 ^a	118.7 \pm 4.23 ^a	114.2 \pm 14.4 ^a	356.1 \pm 47.38 ^b
<i>F</i> – value (df 5,18)	22.03 ^{**}	42.58 ^{**}	15.39 ^{**}	33.55 ^{**}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference ($p < 0.01$).

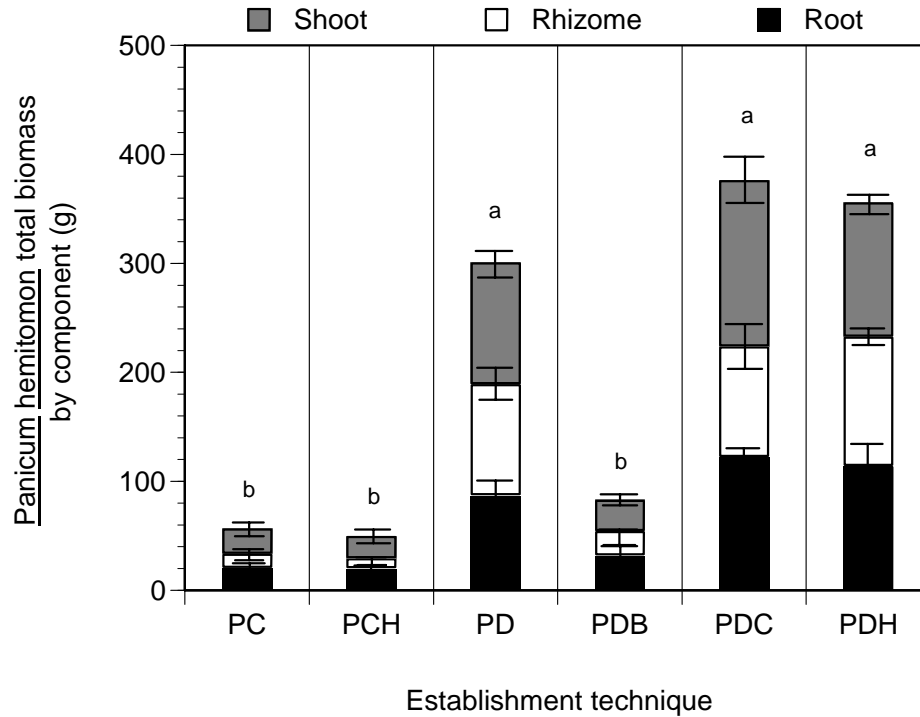


Figure 4.8. The effect of establishment technique on *Panicum hemitomon* total biomass (g) partitioned by component (shoot, rhizome, and root). Treatment codes are as follows: PC = *Panicum hemitomon* in chicken wire; PCH = *Panicum hemitomon* in chicken wire with humic acid amendment; PD = *Panicum hemitomon* in Duralast coconut fiber with peat; PDB = *Panicum hemitomon* in Duralast coconut fiber with bagasse; PDC = *Panicum hemitomon* in Duralast coconut fiber with peat and canvas underpinning; PDH = *Panicum hemitomon* in Duralast coconut fiber with peat and humic acid amendment. Values are means \pm SE ($n = 4$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{5,18} = 33.55$, $p < 0.0001$).

Total mat biomass per multi-species treatment (Table 4.4), taking into account the individual masses of Panicum hemitomom and each secondary species when present, exhibited a highly significant treatment effect ($F_{6,21} = 15.77$, $p < 0.0001$), ranging from 248.20 g (PhHr treatment) to 995.72 g (PhLp treatment). Importantly, this difference was observed despite the fact that Panicum hemitomom total biomass did not vary significantly across treatments, indicating that there was tremendous variation in the amount of biomass produced by select secondary species. Another interesting feature of these data is that for the four and five species combinations (the Panicum hemitomom with all edge species treatment and the Panicum hemitomom with all species treatment respectively), Panicum hemitomom attained greater biomass than did species like Ludwigia peploides and Alternanthera philoxeroides, with quite the opposite relationship observed when these same species in two-species combinations were evaluated.

Table 4.4. Total biomass (g) for all species per multi-species treatment. Columns represent plant tissue dry mass (g), whereas rows represent specific treatment combinations. Column codes are as follows: A.p. = *Alternanthera philoxeroides*; H.r. = *Hydrocotyle ranunculoides*; L.p. = *Ludwigia peploides*; P.h. = *Panicum hemitomon*; S.l. = *Sagittaria lancifolia*. Row codes are as follows: PD = *Panicum hemitomon* only; PhAp = *Panicum hemitomon* with *Alternanthera philoxeroides*; PhHr = *Panicum hemitomon* with *Hydrocotyle ranunculoides*; PhLp = *Panicum hemitomon* with *Ludwigia peploides*; PhSl = *Panicum hemitomon* with *Sagittaria lancifolia*; Ph all = *Panicum hemitomon* with all species (including *Sagittaria lancifolia*); Ph edge = *Panicum hemitomon* with all edge species (excluding *Sagittaria lancifolia*). Values are means above (SE) (n = 4).

Treatment	Plant species					Totals
	A. p.	H. r.	L. p.	P. h.	S. l.	
Ph	----	----	----	300.99 ^a (34.46)	----	313.49 ^c (29.29)
PhAp	466.81 ^a (61.03)	----	----	263.80 ^a (95.37)	----	732.55 ^b (180.03)
PhHr	----	15.3 ^a (6.63)	----	232.90 ^a (38.77)	----	248.20 ^d (46.87)
PhLp	----	----	764.3a (78.95)	231.87 ^a (17.25)	----	995.72 ^a (158.13)
PhSl	----	----	----	280.35 ^a (48.13)	55.48 ^a (16.88)	338.48 ^c (51.44)
Ph all	138.50 ^b (24.28)	9.39 ^a (3.66)	209.95 ^b (82.60)	230.96 ^a (22.70)	28.17 ^a (3.49)	616.97 ^b (222.75)
Ph edge	121.45 ^b (36.94)	4.38 ^a (1.28)	166.85 ^b (41.79)	259.00 ^a (33.68)	----	551.90 ^b (117.79)
F– value (df 6,21)				1.27 ^{NS}		15.77 ^{**}
F– value (df 2,11)	19.30 ^{**}	1.54 ^{NS}	22.50 ^{**}			
F– value (df 1,7)					2.48 ^{NS}	

^a Means with the same letter in the same column are not statistically different (p < 0.05) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference (p < 0.01); ^{NS} non-significant difference (p > 0.05).

Panicum hemitomom total rhizome length and estimated root volume for the multi-species treatments exhibited opposing trends with respect to statistical significance (Table 4.5). Rhizome length varied significantly ($F_{6,21} = 2.87$, $p = 0.0335$), with the Panicum hemitomom only treatment exhibiting the greatest rhizome length, and treatments such as Panicum hemitomom with Ludwigia peploides and Panicum hemitomom with all edge species, representing the smallest rhizome lengths.

As would be expected based on non-significant differences in root biomass, estimated root volume, ranging from 451.1 cm³ (PhHr treatment) to 561.4 cm³ (PhSI treatment), did not vary significantly across treatments. The variation in root volume largely confers with the variation observed in root biomass, as root biomass was used in estimating root volume.

Table 4.5. *Panicum hemitomom* total rhizome length (m) and estimated root volume (cm³) for each multi-species treatment. Treatment codes are as follows: Ph = *Panicum hemitomom* only; PhAp = *Panicum hemitomom* with *Alternanthera philoxeroides*; PhHr = *Panicum hemitomom* with *Hydrocotyle ranunculoides*; PhLp = *Panicum hemitomom* with *Ludwigia peploides*; PhSI = *Panicum hemitomom* with *Sagittaria lancifolia*; Ph all = *Panicum hemitomom* with all species (including *Sagittaria lancifolia*); Ph edge = *Panicum hemitomom* with all species (excluding *Sagittaria lancifolia*). Values are means \pm SE (n = 4).

Treatment	<i>Panicum hemitomom</i> total rhizome length (m)	<i>Panicum hemitomom</i> estimated root volume (cm ³)
Ph	45.5 \pm 4.07 ^a	504.5 \pm 100.29 ^a
PhAp	35.4 \pm 5.83 ^{ba}	546.05 \pm 94.39 ^a
PhHr	32.5 \pm 3.27 ^{ba}	451.1 \pm 38.67 ^a
PhLp	28.9 \pm 2.60 ^b	505.7 \pm 26.36 ^a
PhSI	39.8 \pm 3.92 ^{ba}	561.1 \pm 90.3 ^a
Ph all	28.4 \pm 2.00 ^b	490.1 \pm 32.36 ^a
Ph edge	34.8 \pm 1.16 ^{ba}	524.5 \pm 37.61 ^a
<i>F</i> – value (df 6,21)	2.87 [*]	0.29 ^{NS}

^a Means with the same letter in the same column are not statistically different (p < 0.05) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{*} Significant difference (p < 0.05); ^{NS} non-significant difference (p > 0.05).

Panicum hemitomom total rhizome length for establishment technique (Table 4.6), ranging from 4.7 m (PCH treatment) to 56.7 m (PDH treatment), exhibited a highly significant treatment effect ($F_{5,18} = 42.72$, $p < 0.0001$). As discussed previously for rhizome biomass, the most interesting finding associated with these data, although not statistically significant, is the 19% increase in rhizome length observed with humic acid amendment. A difference of 19% translates into approximately 11 m of overall rhizome length.

Estimated root volume, ranging from 118.0 cm³ (PCH treatment) to 706.5 cm³ (PDC treatment), also varied significantly across establishment technique ($F_{5,18} = 15.39$, $p < 0.0001$ respectively). Because they are correlated, estimated root volume exhibited a similar pattern to that of root biomass, and although root volume exhibited a similar beneficial effect of humic acid, it does not carry the same ecological significance as does rhizome length because of the estimation factor.

Table 4.6. Panicum hemitomom total rhizome length (cm) and estimated root volume (cm³) for each establishment technique. Treatment codes are as follows: PC = Panicum hemitomom in chicken wire; PCH = Panicum hemitomom in chicken wire with humic acid amendment; PD = Panicum hemitomom in Duralast coconut fiber with peat; PDB = Panicum hemitomom in Duralast coconut fiber with bagasse; PDC = Panicum hemitomom in Duralast coconut fiber with peat and canvas underpinning; PDH = Panicum hemitomom in Duralast coconut fiber with peat and humic acid amendment. Values are means \pm SE (n = 4).

Treatment	<u>Panicum hemitomom</u> total rhizome length (m)	<u>Panicum hemitomom</u> estimated root volume (cm ³)
PC	5.7 \pm 0.99 ^b	119.8 \pm 29.88 ^b
PCH	4.7 \pm 1.13 ^b	118.0 \pm 24.83 ^b
PD	45.5 \pm 4.07 ^a	504.5 \pm 100.29 ^a
PDB	10.7 \pm 3.9 ^b	184.9 \pm 72.90 ^b
PDC	49.0 \pm 4.08 ^a	706.4 \pm 73.04 ^a
PDH	56.7 \pm 5.53 ^a	659.7 \pm 83.70 ^a
<i>F</i> – value (df 5,18)	42.72 ^{**}	15.39 ^{**}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference ($p < 0.01$).

Discussion

This experiment combined key findings from earlier experiments with an evaluation of both a multi-species approach for creating thick-mat floating marsh, and a suite of Panicum hemitomon establishment techniques. Duralast coconut fiber served as the sole mat or containment material in all but two treatments, whereas peat (i.e., ground sphagnum peat moss) served as the sole substrate material for all multi-species treatments. This combination was also used for three of the establishment techniques because it was determined from earlier experiments (Chapter 3) to be the most suitable combination. Additional treatments that did not include Duralast coconut fiber and peat in combination, were tested either to evaluate potentially more cost-effective approaches, as in the case of the two chicken-wire treatments, or to utilize a readily available agricultural byproduct, as in the case of bagasse. Overall, this experiment achieved its primary objective in that its results support the use of, or in some cases the abandonment of, particular strategies for enhancing floating marsh restoration. In a few instances, such as with facilitation, or the apparent growth benefits of humic acid amendment, results are suggestive, but require additional study under field or controlled-setting conditions.

As detailed in the introduction of this chapter, the role of species diversity and multi-species planting approaches on ecosystem-level processes, particularly their influence on the restoration of ecosystem function, is well demonstrated in the ecological literature (Ewel et al. 1991; Naeem et al. 1994; Tilman and Downing 1994; Johnson et al. 1996; Naeem and Li 1997; Tilman 1997; Tilman et al. 1997; Symstad 2000; McKee et al. 2007). Evidence also exists linking multi-species planting approaches to the amelioration of specific edaphic parameters, and to more physical attributes of vegetation structure (Zedler et al. 2001; Calloway et al. 2003; Zedler 2005; McKee et al. 2007). In this research, the proportion of total area vegetated provided an initial metric, albeit cursory, as to which multi-species combination, or

establishment technique, was most beneficial from a marsh restoration perspective. Other data, including Panicum hemitomon total biomass, created mat total biomass, and root morphological data, support the vegetative cover data in recommending the Panicum hemitomon with Ludwigia peploides combination as a means for enhancing floating marsh restoration.

Considering the primary objective of this experiment (i.e., evaluating multi-species methods for enhancing the vegetative development of created floating marsh), I assumed that treatments with a greater number species, or a higher density of planting units, would be advantageous over treatments with fewer species, particularly if the candidate species minimized direct competition for resources by exhibiting explicitly different growth forms. Although the effects of inter-specific competition and competitive exclusion on plant growth and performance are well documented (Connell and Slatyer 1977; Grime 1979; Tilman 1982), I was unsure at the outset of this experiment whether any of the species I employed would exhibit superiority because none exhibited growth characteristics suggestive of such an outcome. Despite the fact that there were significant differences in total mat biomass, Panicum hemitomon total biomass did not vary significantly as expected. However, competitive interactions were present because patterns, but not always statistically significant trends, were observed for partitions of Panicum hemitomon biomass across treatments. The decrease in Panicum hemitomon rhizome growth (but not root growth) for the Panicum hemitomon with Ludwigia peploides treatment is an important finding that could have implications for mat structural integrity and buoyancy, in addition to the obvious effects on Panicum hemitomon lateral spread.

As noted in the project objectives, I hypothesized that one or more of the laterally-growing specialists may facilitate the establishment of Panicum hemitomon. Based on these

data, facilitation does not appear to be occurring because the proportion of total area vegetated by Panicum hemitomon was greatest for the Panicum hemitomon only treatment, and second greatest, at least among the treatments that included laterally-growing edge specialists, was the Panicum hemitomon with Hydrocotyle ranunculoides treatment, a combination that was dominated by Panicum hemitomon. I recognize now however that facilitation would be difficult to accurately detect in such a short-term study, as this is a process that may not become evident for several growing seasons. Such effects would be more effectively assessed in a longer-duration field experiment.

Minimum nutrient requirements vary by species (Chapin 1980), but it is doubtful that such effects significantly affected the outcomes observed here. Rather, it seemed that insufficient transplanting resiliency, and other stressors associated with constant hydrologic inundation, were more responsible for certain species performing poorly. Although it is plausible that the condition of poorly-performing species could have improved over time, five months of growth seemed sufficient for evaluation purposes considering the time-sensitive context of wetland restoration (i.e., the need to establish plants as quickly and effectively as possible). I concluded that stem fragility, and lack of transplanting resilience, was a major obstacle affecting Hydrocotyle ranunculoides survivorship, whereas Alternanthera philoxeroides, despite its moderately good performance, may ultimately prefer more mesic conditions with improved aeration. Sagittaria lancifolia was expected to prosper in the created mats because it is tolerant of prolonged flooding (Chabreck 1972; Stutzenbaker 1999; Martin and Shaffer 2005; Spalding and Hester 2007). Despite these assumptions, Sagittaria lancifolia performed very poorly, losing a substantial amount of biomass, particularly aboveground biomass, over the course of the experiment. Interestingly though, upon harvest of mats in which Sagittaria lancifolia was planted, a considerable amount of new biomass was observed suspended in the

water column under each mat, all associated with tubers that were initially planted.

Nevertheless, Sagittaria lancifolia grew less than expected for a species that, at times, exhibits co-dominance in naturally-formed thick-mat floating marsh, conditions that I seemed to have closely duplicated in the mats I created. Considering that no con-specifics were used in this experiment, that all treatments were exposed to full-light conditions, and that each species exhibited a different growth form, it seems reasonable to infer that incidental shading was not a major factor in any particular species performing poorly.

After one month of growth, it became clear that Ludwigia peploides found conditions in the created mats most accommodating. When compared to all other species except Panicum hemitomon, Ludwigia peploides demonstrated the greatest resistance to transplanting stress, despite having not been propagated. Ludwigia peploides exhibited rapid growth within days of being planted, and had it not been for the moderate insect-induced defoliation event between the July and August samplings, it is likely that Ludwigia peploides total cover and biomass would have been considerably greater at harvest. I also suspect that Ludwigia peploides would have attained greater biomass had it not been for size limitations of the experimental vessels. Overall, Ludwigia peploides exhibited vigorous growth, and unlike each of the other laterally-growing edge specialists, extensively colonized interior portions of created mats, thereby contributing substantially to their structural integrity, an effect that was most apparent at harvest when rhizome and root biomass was recovered from the Duralast coconut fiber.

The propensity for extensive lateral growth, and the tendency for each stolon to subdivide into multiple stolons, makes Ludwigia peploides a superior choice for thick-mat floating marsh restoration. This notion is further supported by the fact that Ludwigia peploides and Panicum hemitomon exhibit different growth forms with respect to both above- and belowground components. With the exception of laterally-growing rhizomes, Panicum

hemitomon grows vertically, whereas Ludwigia peploides is a low stature herbaceous species that grows exclusively across the surface of the water (Godfrey and Wooten 1979a and 1979b). Unlike the slender leaf blades and tightly-arranged canopy of Panicum hemitomon, the leaves of Ludwigia peploides are obovate, and occur in small clusters, emerging from each stem node. As for rhizome (and stolon) growth, rhizomes of Panicum hemitomon typically occur belowground, or in this case within created mats or beneath the surface of the water, whereas stolons of Ludwigia peploides occur almost exclusively aboveground, or in this case on the surface of created mats and the water. Identifying such morphological differences was of interest not simply for reasons associated with mat structural integrity, but as a potential means for enhancing the fusion or coalescence among adjacent created mats (if deployed in a field setting). The fact that Ludwigia peploides exhibited extensive lateral growth is not the only trait that makes it attractive from a floating marsh restoration perspective. Root morphological attributes also appeared promising for creating vegetatively integrated and structurally-sound thick-mat floating marsh.

One potentially important caveat to the before mentioned benefits is the unexpected and diminished rhizome growth exhibited by Panicum hemitomon when grown in conjunction with Ludwigia peploides. Because Panicum hemitomon is predominantly a clonal species, rhizome growth is an important aspect of its lateral spread, which itself is an important aspect of floating marsh structural integrity and buoyancy. Despite the 19% reduction (equivalent to approximately 11 m of length) in rhizome growth for this species combination, it is possible that the enhancing qualities of increased root biomass and increased coalescence potential afforded by Ludwigia peploides, compensates for the diminished Panicum hemitomon rhizome growth. I feel, if for no other reason than for basic ecological knowledge, that further elucidation of this relationship is warranted.

Treatments with greater than two species were not associated with the greatest proportion of total area vegetated, nor were they associated with the greatest total mat biomass, although all two-species treatments did exhibit greater cover than did the Panicum hemitomom only treatment. In these treatments, species such as Ludwigia peploides and Alternanthera philoxeroides, but predominantly Ludwigia peploides, were clearly dominant. The Panicum hemitomom with all edge species (excluding Sagittaria lancifolia) and the Panicum hemitomom with all species (including Sagittaria lancifolia) treatments, despite including a greater number of species (4 and 5 respectively), were associated with less vegetative cover and less total mat biomass as compared to both the Panicum hemitomom with Ludwigia peploides and the Panicum hemitomom with Alternanthera philoxeroides treatments. The dominance of Ludwigia peploides was further substantiated by the fact that it independently accounted for the greatest proportion of total cover in the four and five-species treatments. Interestingly however, when individual plant total biomass is considered, Ludwigia peploides was dominant among secondary species in these treatments, but it was superseded by Panicum hemitomom in both treatments once all species contributions were accounted for.

Considering Panicum hemitomom vegetative cover and mat total biomass with respect to establishment technique, there were good-performing and poorly-performing treatments. Treatments that included Duralast coconut fiber and peat were good-performing, whereas poorly-performing treatments all lacked one or both of these materials. As mentioned in the Results section, the most notable outcomes for the establishment techniques were the minimal growth observed under hydroponic conditions, the poor response of Panicum hemitomom when grown in bagasse, the apparent benefit of humic acid with respect to Panicum hemitomom rhizome growth, and to a lesser degree, the notion of a more robust root mat achieved via root directional impedance.

Species with root systems that have the potential to bolster mat structural integrity are most desirable from the perspective of marsh restoration, whereas root tissue that is sufficiently buoyant is not simply desirable, but imperative so as to not negatively affect marsh buoyancy. In addition to satisfying all other requirements, Ludwigia peploides is the only secondary species that also sufficiently met these requirements. Roots of Alternanthera philoxeroides, Hydrocotyle ranunculoides, and Sagittaria lancifolia, all appeared ineffective at contributing to the overall strength of created as inferred from root morphology. Each of these species, but particularly Hydrocotyle ranunculoides and Alternanthera philoxeroides, produced roots that lacked significant rigidity, or roots that essentially lacked the capacity for lateral growth. Alternatively, Ludwigia peploides rooted extensively into and through created mats, produced roots with many first-order laterals, and exhibited sufficiently buoyant downward-growing roots. The low specific gravity, foam-like structures that envelop upward-growing Ludwigia peploides roots appear to provide much needed support for laterally-growing stolons (Ellmore 1981). Ellmore (1981) described upward-growing Ludwigia peploides roots and concluded that despite their delayed development, and the fact that they often become enveloped in a foam-like material, they perform similar physiological functions as downward-growing roots. These characteristics, in addition to others discussed earlier, make Ludwigia peploides, of the species evaluated in this experiment, a preferable choice for thick-mat floating marsh restoration.

From a controlled-setting perspective, this research supports the notion of using a multi-species approach for augmenting thick-mat floating marsh restoration. It also provides data in support of at least one avenue for enhancing the establishment of Panicum hemitomon. It appears that the inclusion of Ludwigia peploides will benefit floating marsh restoration because growth on its part does not appear to be entirely at the expense of vigorous Panicum hemitomon growth, although clearly trade-offs do exist. Furthermore, the deliberate inclusion

of a rapidly-growing species such as Ludwigia peploides may reduce the probability of colonization by less desirable species that may compete more rigorously with Panicum hemitomon, or disrupt mat stability prior to achieving high vegetative cover of Panicum hemitomon.

Chapter 5

Conclusions

Project objectives revisited

Floating marshes are an important constituent of the wetland mosaic of coastal Louisiana, and while their degradation and loss has not gone unrecognized, the knowledge required to make informed decisions about how to go about restoring them has been largely insufficient. Because floating marshes are considerably different than more typical attached marshes in terms of formation and maintenance, strategies and techniques employed elsewhere are generally of little or no use for their restoration. Resulting from incomplete knowledge, and continued floating marsh degradation and loss, as well as concerns over future management, a large multi-institutional effort (LA-05-Floating Marsh Creation Demonstration Project), including both field and controlled-setting experiments, was launched to elucidate key biotic and abiotic constraints on plant establishment and growth within a floating marsh restoration context. Equally as important and ongoing, structural designs are being developed that, when combined with the plant response data reported herein, are intended to represent designs ready for field testing. The research contained herein, and the conclusions that are presented in this section, represent key plant responses generated under controlled conditions.

Crucial to developing a protocol for floating marsh restoration is identifying how the dominant macrophyte of thick-mat floating marsh, and consequently the focal species of all restoration efforts, Panicum hemitomon, responds in terms of growth and patterns of biomass allocation to conditions associated with the restoration process. Importantly, and to the extent possible, each experiment that I carried out built upon key findings from previous experiments.

The product was a largely independent body of work that represents one of the most complete assessments of ecophysiological aspects of floating marsh restoration to date.

Nutrient and hydrologic effects

The assessment of Panicum hemitomon growth response and patterns of biomass allocation as influenced by nutrient loading rate and hydrologic regime yielded plant-level response data are of direct use for floating marsh restoration. The nutrient data suggested that, while Panicum hemitomon biomass largely benefited from nutrient enrichment, particularly nitrogen enrichment ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$), such loading rates might not be required for vigorous Panicum hemitomon growth, or for successful floating marsh restoration. The loading rates employed here were significantly greater than background loading rates associated with Panicum hemitomon-dominated floating marshes, or for other freshwater wetlands not near diversion outfalls. Nitrogen loading rates in these and other regional freshwater marshes vary with depth, and based on contact with the free water under the floating mat, but are generally less than $8 \text{ g N m}^{-2} \text{ yr}^{-1}$ (DeLaune et al. 1986; Bowden 1987; Sasser 1994). Thus, and compared to background loading rates, the non-enriched loading rate for the experiments I conducted represents nearly a three-fold increase, whereas the enriched loading rate ($50 \text{ g N m}^{-2} \text{ yr}^{-1}$) represents more than a five-fold increase. In other words, the greater shoot, rhizome, and root biomass exhibited by Panicum hemitomon grown under nitrogen enrichment is far greater than what would be expected under normal loading rates in these wetlands. Not only is such enrichment not necessary, but administering such loading rates is not advisable from an ecological perspective. In fact, such loading rates, despite greater biomass, resulted in shifts in allocation patterns, notably less belowground biomass relative to aboveground biomass. Although small, and not statistically significant, this effect could have been more pronounced over time, and is therefore not encouraging if the objective is to foster conditions that promote

rhizome and root growth to the extent possible. As a result, I recommend the lower loading rate even though it is still a increase over normal background levels. I recognize that it may be advantageous, in some cases, to fertilize newly-created vegetated mats with a greater-than-needed loading to jump-start vigorous Panicum hemitomom growth and to increase stress tolerance. Such fertilization should be achievable using the non-enriched rates presented here. If additional applications are needed, not only should they be based on deficiencies as inferred from plant performance, but they might be achieved using even a lower loading rate.

One of the factors that influenced my decision to choose the loading rates employed here was an interest in better understanding how Panicum hemitomom patterns of biomass allocation would shift in response to eutrophication. Eutrophication is occurring in coastal Louisiana, and there is concern over the long-term effects on recipient wetlands. Considering this, the shifts in biomass allocation that I observed under nitrogen enrichment, and the potential for accelerated organic matter decomposition, there is reason for concern regarding the long-term sustainability of marshes, floating marshes included, near nutrient-rich river diversions. Although phosphorous enrichment ($10 \text{ g P m}^{-2} \text{ yr}^{-1}$) enhanced Panicum hemitomom rhizome and root growth, at least under saturated hydrologic conditions, I unfortunately have less of a basis to make an informed decision regarding a recommended loading rate for phosphorous. Phosphorous loading at the levels administered in this research is likely to have less of an impact on the vegetative community as compared to nitrogen, and as a result, I cautiously recommend the lower loading rate. However, I strongly feel that field trials in a community setting are needed to better understand community-level responses to eutrophication. Only then, when combined with this species-level growth response data, may specific loading rates for these two nutrients be declared.

Unlike nutrient regime, relatively clear inferences can be drawn from Panicum hemitomom growth response as influenced by hydrologic regime, notably that saturated hydrologic conditions were significantly more conducive for vigorous growth than inundated conditions. Regardless of nutrient regime, inundation severely retarded Panicum hemitomom growth, particularly rhizome and root production, suggesting that excessive flooding is unadvisable for restoring floating marsh. Interestingly, the results reported herein do not agree unanimously with several earlier studies that observed enhanced Panicum hemitomom growth in inundated conditions (15 cm of flooding). This is not to say that some level of flooding greater than saturation (i.e., flooded to the surface of the root mat) is not beneficial because the conditions in which the created mats were housed in this study could have accentuated the degree of flooding-induced stress. What is meant by this is that while there was a free-water zone under each vegetated mat, they nevertheless fit tightly into each experimental vessel. Therefore, more reduced or oxygen-limited conditions could have affected the rooting environment at depth, particularly in the free-water zone where aeration was likely very poor, but where measurements were not taken. All interstitial measurements were performed in vegetated mats, not at greater depths in the free-water zone. In a field or restoration setting, I suspect that such conditions would be less likely to develop, as least initially, due to hydrologic exchange with surrounding water bodies.

Synthesizing findings for nutrient and hydrologic regimes, I recommend that saturated hydrologic conditions (i.e., flooded to the surface of the vegetated mat) be strived for in a restoration setting. Regardless of nutrient regime, saturated conditions resulted in more vigorous growth as compared to inundated conditions. Moreover, if saturated conditions represent the hydrologic 'target', but over time slightly more flooding is experienced, there should be less reason for concern on the part of resource managers knowing that Panicum

hemitomon is tolerant, and by some accounts, enhanced by moderate flooding (5 to 10 cm).

With respect to nutrient effects, the non-enriched conditions ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$) in this study were greater than background conditions in a typical freshwater wetland. Therefore, and although these rates are recommended for fertilization, it is important to keep in mind that such applications may not need to be administered over the long term, rather at initiation, and perhaps periodically thereafter based solely on plant performance.

Substrate and mat or containment materials

Despite the fact that it has been hypothesized that substrates required for floating marsh restoration need to be both plant-derived and buoyant (Sasser et al. 1993), little effort has been devoted to identifying, much less experimentally testing, candidate materials. Even less time had been devoted to testing different mat or containment materials. I designated as one of my research objectives the elucidation of these two important knowledge voids, and by doing so, have come to the conclusion that peat and peat-containing blended substrates (i.e., those with $\geq 50\%$ peat content by volume), at least of the substrate materials tested, are best for vigorous Panicum hemitomon growth. I also propose that Duralast coconut mat material be employed as a means for containing the peat-based substrates. I have come to this conclusion not solely based on plant performance, but also by way of structural integrity, recognizing the superior ability of Duralast coconut fiber to contain fine-textured substrates. The fact that it is a natural-fiber product free of synthetic materials also makes it attractive.

Although these conclusions would be more substantial if not for incomplete results owing to Hurricane Katrina, peat and peat-based materials resulted in a rooting environment more conducive to vigorous Panicum hemitomon growth. Not only was interstitial pH slightly more acidic for peat-based materials, a condition Panicum hemitomon seems to tolerate supported by field data, but these materials exhibited less-reduced redox potentials and lower

COD, suggesting a less oxygen-limited rooting environment. Duralast coconut fiber is densely spun latex-coated coconut fiber that averages between 3 and 5 cm. The result is a rigid, yet flexible, material that significantly augments the creation of a strong root mat because the foundation for such a mat is present prior to planting. Duralast coconut fiber is resistant to tearing when new, but as gathered from the experiments I performed, seems to be susceptible to ultra-violet deterioration. As a result, the structural lifespan of Duralast coconut fiber is relatively short term (approximately 3 years). I view such qualities as beneficial because, based on experience, by the time such materials no longer exhibit structural integrity (i.e., 3 years), a vigorously-growing plant community, and a self-supportive root mat, should be in place.

I feel that these data are useful for floating marsh restoration, however, I recognize that the ecological footprint of restoring floating marsh could be made smaller if peat was blended with another organic material, either a byproduct of another plant-based industry similar to that of sugarcane, or one that utilizes materials that are not commercially harvested as peat is. I also realize that Duralast coconut fiber, although performing best in this experiment, may not be cost-effective on large spatial scales. As a result, there is merit in identifying substitutes that achieve the same level of plant vigor, containment ability, and mat strength, keeping in mind, however, that ecological restoration may not always be a cost-effective venture. In the interim, and based on this research, the peat and Duralast coconut fiber combination is recommended.

Multi-species effects

Panicum hemitomon is required for creating and restoring thick-mat floating marsh. However, it is well known that floating marshes are species rich, a portion of which are laterally-growing edge species. My desire to quantitatively evaluate a multi-species approach for augmenting floating marsh vegetative development, one that included laterally-growing edge species, provided a significant amount of insight regarding restoration. Initially, data

obtained from the multi-species experiment supported earlier findings for creating mats using peat and Duralast coconut fiber in combination. Moreover, the multi-species experiment confirmed that non-enriched nitrogen and phosphorous loading rates ($25 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $5 \text{ g P m}^{-2} \text{ yr}^{-1}$) are more than sufficient for vigorous Panicum hemitomon growth. Vigorous growth refers to the robust rhizome and root growth required for mat formation, and the robust shoot growth that is required for the habitat-providing services afforded by floating marsh. Next, this experiment lead me to conclude that floating marsh restoration can be augmented by the inclusion of laterally-growth edge specialists such as Ludwigia peploides, recognizing however, that trade-offs may exist between partitions of Panicum hemitomon production and beneficial attributes of accompanying secondary species. Despite reduced Panicum hemitomon lateral spreading potential as inferred from diminished rhizome growth, the Panicum hemitomon with Ludwigia peploides combination resulted in the greatest vegetative cover and mat biomass. Ludwigia peploides also contributed substantially to the structural integrity and buoyancy of created mats by producing a tremendous amount of branched and buoyant roots, with its stolons readily colonizing both mat and open-water areas. Based on the lateral spreading potential as inferred by the length and rooting potential of its stolons, Ludwigia peploides also appears promising for enhancing the coalescence of adjacent created mats in field settings. Although an unplanned effect, Ludwigia peploides is particularly attractive from a restoration perspective because of its resiliency to moderate herbivore-induced defoliation, having rebounded to near pre-disturbance vegetative cover in a relatively short period of time (approximately four weeks).

Establishment techniques

Gathered from this assessment of establishment technique, a hydroponic approach for establishing Panicum hemitomon does not appear to be overly effective (although forthcoming

data from field trials using rhizome and root fragments may counter this assertion). Various Panicum hemitomom biomass-related metrics responded to humic acid amendment, and to root directional impedance, although it is open for debate whether such responses are ecologically significant, or otherwise worthy of further elucidation. Considering this, as well as the required pre-deployment resources and man-hours spent constructing individual floating mats, much less outfitting them with root directional impedance devices, humic acid amendment appears more promising, as it is inexpensive and easy applied as a foliar spray. I feel that it would be especially interesting to further assess humic acid amendment in a multi-species setting, such as one in which floating mats planted with Panicum hemitomom and Ludwigia peploides could be rigorously evaluated. At this point, however, neither of these approaches is recommended for restoration purposes, although it would be of benefit to use a small number of vegetated mats in an actual restoration project for a pilot study to further assess humic acid amendment under field conditions.

Project synthesis

Despite the before mentioned advances brought about by this doctoral research, it and the results as described in this dissertation, are not without limitations. I recognize that all of the studies I carried out were under controlled conditions, and that administering and adhering to a specific fertilization regime for example, or maintaining precise hydrologic conditions, present formidable challenges in non-controlled field settings. Considering this, it may be most appropriate to interpret the findings and recommendations as presented here for vigorous Panicum hemitomom growth as 'restoration targets' because slight deviation from such targets is not likely to significantly compromise project success. Managing unwanted or undesirable plant species, particularly species that are superior competitors or woody species, such as Morella cerifera (L.) Small, that have the potential to negatively affect marsh buoyancy, is also an area

of concern. Likewise, the effective exclusion of Myocastor coypus (nutria) from restoration sites has proven to be challenging, and is therefore important for successful restoration. However, as evident in my desire to incorporate multiple plant species in the restoration design, I am not suggesting that all voluntarily-arriving plant species are undesirable, as naturally-formed floating marsh is generally quite species rich (≥ 20 species is not uncommon). Although attaining a species-rich marsh is a long-term goal of this restoration effort, it is initially important to establish species that define thick-mat floating marsh, as well as ones that positively contribute to root mat development and buoyancy.

When viewed collectively, this doctoral research achieved two important objectives. First, it generated information that advances the body of ecological knowledge for a common freshwater plant in Panicum hemitomon. Although Panicum hemitomon is confined to freshwater areas only, and despite the fact that floating marsh is a wetland ecosystem with many inherently unique attributes, Panicum hemitomon happens to be a candidate species for a variety of restoration-oriented applications because it is easily propagated from cuttings and rhizome fragments, resistant to transplanting stress, and forms dense and fibrous root networks. Hence, my research is likely to benefit restoration projects other than those associated with floating marsh that employ Panicum hemitomon as the focal species. Importantly, this research also demonstrates how this plant may respond to hydrologic fluctuations and enriched nutrient availability, forcing factors that are likely to be of greater ecological concern in coastal Louisiana in the future. Second, all of the experiments described herein were conducted in such as way as to contribute to the development of a means for creating, and ultimately restoring, thick-mat floating marsh.

Having said this, and despite minor limitations, I feel that the data as presented here are of significant value, but of even greater value, when combined with findings associated with

thin-mat floating marsh restoration, and with field-trial data currently being produced by collaborators at the Coastal Ecology Institute in the School of the Coast and Environment at Louisiana State University. Of particular interest are natural-fiber floatation devices designed for supporting vegetated mats, maintaining appropriate flooding depths, and for minimizing herbivore disturbance. I feel confident that when the research and monitoring phases associated with this project are complete, that resource managers will possess the knowledge necessary to successfully restore thick-mat floating marsh in coastal Louisiana. These controlled-setting studies have largely met their objectives regarding protocol development. Much of the fine-tuning, and longer-to-develop processes and physical attributes associated with restoration, are not likely to become evident until field deployment occurs.

Future directions

As alluded to in the synthesis, extensive field studies testing structural designs and field-based plant responses are ongoing for floating marsh restoration. Combining the controlled-setting data that I generated, with field data when available, will provide an enormous amount of insight, and likely the information necessary for creating and restoring floating marsh. From my controlled-setting perspective, the most fruitful direction I see regarding future science is further elucidation of the multi-species planting approach, particularly the testing of such combinations in unconstrained field conditions, and under conditions with more competitive interactions. Coupling future multi-species assessments with different nutrient regimes, most notably nutrient enrichment, would be of interest from a restoration perspective, as well as from a wetland management perspective, considering the future concern over eutrophication in coastal Louisiana. Elucidating nutrient induced shifts in plant composition and dominance, in the event that they actually occur, would be valuable for anticipating and managing future change in freshwater floating marshes.

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Appendix

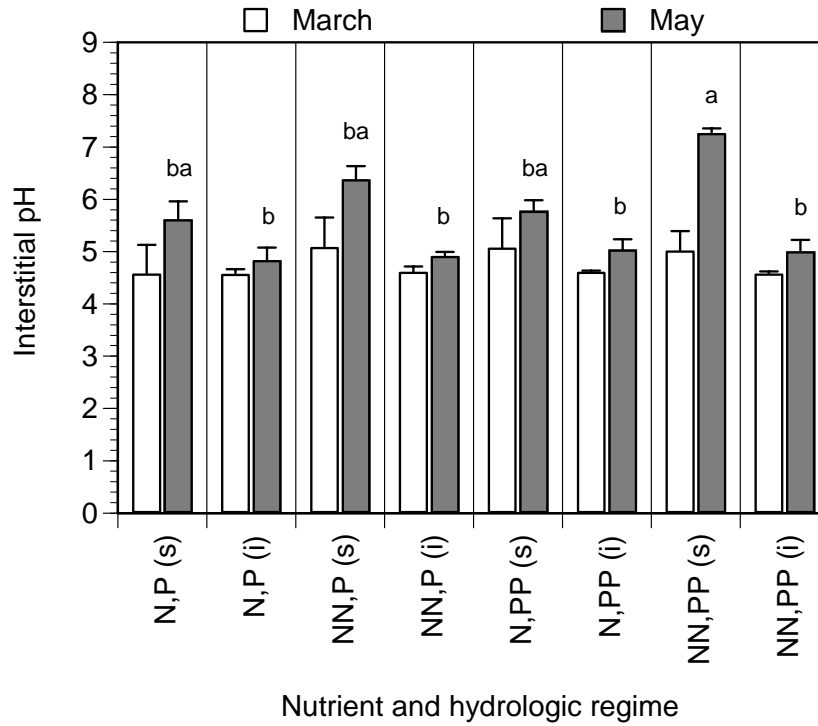


Figure 1. The effect of manipulated nutrient availability and hydrology on substrate interstitial pH for the phase – II study (Chapter 2), measured in March and May of 2006. Treatment codes are as follows: N = low nitrogen; NN = high nitrogen; P = low phosphorous; PP = high phosphorous; s = saturated; i = inundated. Values are means \pm SE ($n = 5$). Statistical significance is as follows: time (Wilks' Lambda: $F_{1,32} = 59.98$, $p < 0.0001$); time by hydrology (Wilk's lambda: $F_{1,32} = 20.13$, $p < 0.0001$); letters over bars represent significantly different means for May data only (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{7,32} = 5.22$, $p = 0.0005$).

Table 1. *Panicum hemitomom* total stem number, total stem height, and mean stem height for phase – I and II (Chapter 2). All measurements were obtained on the final round of aboveground sampling after four months of growth. Values are means \pm SE (n = 5).

Phase – I			
Treatment	Total stem number (#)	Total stem height (cm)	Mean stem height (cm)
N,P (saturated)	16.0 \pm 1.48 ^c	535.1 \pm 66.30 ^b	34.5 \pm 4.69 ^c
N,P (inundated)	22.8 \pm 3.90 ^c	1049.4 \pm 184.97 ^b	45.8 \pm 2.59 ^{bc}
NN,P (saturated)	21.0 \pm 0.83 ^c	927.5 \pm 64.98 ^b	44.1 \pm 2.25 ^{bc}
NN,P (inundated)	22.0 \pm 3.27 ^c	996.6 \pm 159.34 ^b	45.3 \pm 2.02 ^{bc}
N,PP (saturated)	26.4 \pm 5.38 ^c	989.1 \pm 205.51 ^b	37.5 \pm 1.40 ^{bc}
N,PP (inundated)	31.6 \pm 2.92 ^{cb}	1557.3 \pm 162.94 ^b	49.0 \pm 1.64 ^{ba}
NN,PP (saturated)	70.6 \pm 7.94 ^a	3461.4 \pm 496.40 ^a	49.1 \pm 3.50 ^{ba}
NN,PP (inundated)	50.8 \pm 4.18 ^b	2978.1 \pm 272.24 ^a	58.6 \pm 2.10 ^a
<i>F</i> – value (df 7,32)	18.92 ^{**}	19.93 ^{**}	7.39 ^{**}

Phase – II			
Treatment	Total stem number (#)	Total stem height (cm)	Mean stem height (cm)
N,P (saturated)	20.2 \pm 2.93 ^{bc}	707.3 \pm 106.37 ^{cd}	51.3 \pm 2.14 ^a
N,P (inundated)	13.6 \pm 2.37 ^c	1012.8 \pm 121.55 ^{bcd}	52.8 \pm 1.58 ^a
NN,P (saturated)	33.8 \pm 3.26 ^a	1178.9 \pm 172.9 ^{bc}	52.5 \pm 2.64 ^a
NN,P (inundated)	19.0 \pm 2.00 ^{bc}	1751.0 \pm 136.8 ^a	61.5 \pm 3.75 ^a
N,PP (saturated)	15.6 \pm 1.20 ^c	539.7 \pm 33.93 ^d	53.6 \pm 1.74 ^a
N,PP (inundated)	9.2 \pm 0.73 ^c	833.6 \pm 58.43 ^{cd}	59.1 \pm 2.06 ^a
NN,PP (saturated)	27.0 \pm 3.74 ^{ba}	1020.4 \pm 72.55 ^{bcd}	57.8 \pm 2.92 ^a
NN,PP (inundated)	17.8 \pm 1.11 ^{bc}	1525.1 \pm 144.0 ^{ba}	57.3 \pm 1.60 ^a
<i>F</i> – value (df 7,32)	10.41 ^{**}	12.56 ^{**}	2.30 ^{NS}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Significant difference ($p < 0.01$); ^{NS} non-significant difference ($p > 0.05$).

Table 2. Line equations and associated levels of significance (R^2 and p-values) from linear regression analyses of Panicum hemitomon PNUE ($\mu\text{mol C g}^{-1} \text{N s}^{-1}$) for phase – I (top portion) and phase – II (bottom portion) (Chapter 2), measured at peak standing crop as a factor of leaf tissue nutrient content (g N cm^{-2}).

<u>Phase – I</u>		
Treatment	Line equation	R^2 (p-value)
N,P (saturated)	$y = 100.7x + -78.94$	0.59 (0.1274)
N,P (inundated)	$y = -81.6x + 115.55$	0.73 (0.0650)
NN,P (saturated)	$y = -77.3x + 109.89$	0.20 (0.4490)
NN,P (inundated)	$y = -31.3x + 60.28$	0.16 (0.4922)
N,PP (saturated)	$y = 4.1x + 16.71$	0.01 (0.8266)
N,PP (inundated)	$y = -0.2x + 29.80$	0.00 (0.9902)
NN,PP (saturated)	$y = -6.0x + 39.68$	0.03 (0.7587)
NN,PP (inundated)	$y = -5.1.x + 35.26$	0.01 (0.8692)
<u>Phase – II</u>		
Treatment	Line equation	R^2 (p-value)
N,P (saturated)	$y = -10.6x + 2.12$	0.39 (0.2534)
N,P (inundated)	$y = -8.1x + 1.65$	0.17 (0.4796)
NN,P (saturated)	$y = 3.3x + 8.55$	0.01 (0.8652)
NN,P (inundated)	$y = 1.5x + 1.01$	0.08 (0.6285)
N,PP (saturated)	$y = 5.4x + 5.46$	0.19 (0.4625)
N,PP (inundated)	$y = -15.2x + 2.09$	0.14 (0.5285)
NN,PP (saturated)	$y = -6.2x + 18.38$	0.82 (0.0322)*
NN,PP (inundated)	$y = -11.3x + 19.83$	0.59 (0.1274)

* Significant difference ($p < 0.05$).

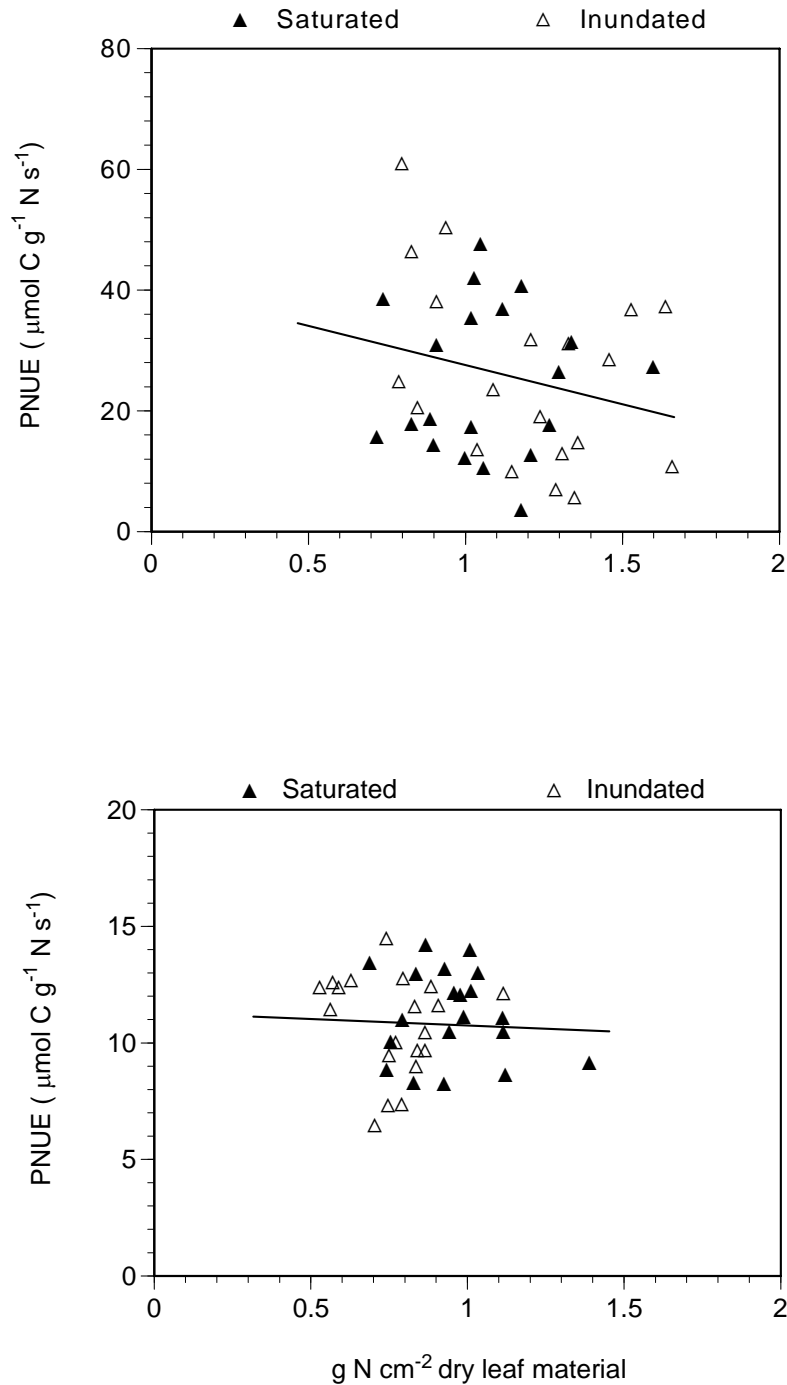


Figure 2. The effect of manipulated nutrient availability and hydrology on *Panicum hemitomon* PNUE (μmol C g⁻¹ N s⁻¹) for phase – I (top panel) and phase – II (bottom panel) (Chapter 2), expressed as a linear regression of PNUE as a factor of leaf tissue nitrogen content (g N cm⁻²). Regression equation and associated r^2 value for phase – I ($y = -11.163x + 38.828$, $r^2 = 0.0415$) and for phase – II ($y = -0.9178x + 11.828$, $r^2 = 0.0061$).

Table 3. *Panicum hemitomom* shoot, rhizome, and root biomass (g) for the phase – II study (Chapter 2) delineated by nutrient and hydrologic regime. All measurements are dry biomass totals obtained after four months of growth (except for rhizome length which was measured on live rhizome tissue at harvest). Values are means \pm SE (n = 5).

<u>Saturated treatments</u>			
Nutrient regime	Stem/leaf biomass (g)	Rhizome biomass (g)	Root biomass (g)
N,P	12.4 \pm 1.98 ^b	4.6 \pm 1.03 ^b	11.3 \pm 1.37 ^{ba}
NN,P	33.4 \pm 2.94 ^a	6.5 \pm 0.81 ^{ba}	15.8 \pm 1.13 ^a
N,PP	12.2 \pm 1.67 ^b	6.3 \pm 0.32 ^{ba}	10.4 \pm 0.67 ^b
NN,PP	31.4 \pm 3.16 ^a	8.6 \pm 0.40 ^a	15.7 \pm 1.26 ^a
<i>F</i> – value (df 3,16)	21.29 ^{**}	5.33 ^{**}	6.17 ^{**}
<u>Inundated treatments</u>			
Nutrient regime	Stem/leaf biomass (g)	Rhizome biomass (g)	Root biomass (g)
N,P	8.89 \pm 1.36 ^b	1.8 \pm 0.55 ^b	6.3 \pm 0.92 ^a
NN,P	24.1 \pm 4.49 ^a	3.2 \pm 0.87 ^a	7.3 \pm 1.11 ^a
N,PP	8.46 \pm 0.35 ^b	1.3 \pm 0.22 ^b	4.8 \pm 0.56 ^a
NN,PP	19.8 \pm 1.03 ^a	3.7 \pm 0.36 ^a	6.4 \pm 0.57 ^a
<i>F</i> – value (df 3,16)	10.69 ^{**}	4.22 [*]	1.57 ^{NS}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Significant difference ($p < 0.01$); ^{*} significant difference ($p < 0.05$); ^{NS} non-significant difference ($p > 0.05$).

Table 4. *Panicum hemitomon* rhizome biomass (g) and rhizome length (cm) for the phase – II study (Chapter 2) delineated by nutrient and hydrologic regime. All measurements are dry biomass totals obtained after four months of growth (except for rhizome length which was measured on live rhizome tissue at harvest). Values are means \pm SE (n = 5).

<u>Saturated treatments</u>		
Nutrient regime	Total biomass (g)	Rhizome length (cm)
N,P	28.5 \pm 3.76	306.0 \pm 72.50
NN,P	55.8 \pm 3.82	393.2 \pm 47.57
N,PP	28.9 \pm 2.20	408.7 \pm 24.94
NN,PP	55.8 \pm 2.60	480.9 \pm 35.80
<i>F</i> – value (df 3,16)	25.45 ^{**}	2.19 ^{NS}
<u>Inundated treatments</u>		
Nutrient regime	Total biomass (g)	Rhizome length (cm)
N,P	17.0 \pm 2.49	103.6 \pm 37.10
NN,P	34.7 \pm 6.32	170.3 \pm 54.42
N,PP	14.6 \pm 0.77	60.92 \pm 8.01
NN,PP	29.9 \pm 0.82	201.8 \pm 15.45
<i>F</i> – value (df 3,16)	8.06 ^{**}	3.50 [*]

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Significant difference ($p < 0.01$); ^{*} significant difference ($p < 0.05$); ^{NS} non-significant difference ($p > 0.05$).

Table 5. Proportional contributions of *Panicum hemitomom* shoot, rhizome, and root biomass to total biomass for the phase – II study (Chapter 2), based on dry biomass totals obtained after four months of growth. Values are means \pm SE (n = 5).

<u>Saturated treatments</u>			
Nutrient regime	Shoot contribution	Rhizome contribution	Root contribuion
N,P	0.43 \pm 0.03 ^b	0.15 \pm 0.02 ^a	0.40 \pm 0.03 ^a
NN,P	0.59 \pm 0.02 ^a	0.11 \pm 0.01 ^a	0.28 \pm 0.01 ^b
N,PP	0.41 \pm 0.02 ^b	0.22 \pm 0.01 ^a	0.36 \pm 0.01 ^{ba}
NN,PP	0.55 \pm 0.03 ^a	0.15 \pm 0.00 ^{ba}	0.28 \pm 0.02 ^b
<i>F</i> – value (df 3,16)	9.12 ^{**}	6.68 ^{**}	5.61 ^{**}
<u>Inundated treatments</u>			
Nutrient regime	Shoot contribution	Rhizome contribution	Root contribuion
N,P	0.52 \pm 0.03 ^b	0.10 \pm 0.02 ^a	0.37 \pm 0.01 ^a
NN,P	0.69 \pm 0.01 ^a	0.08 \pm 0.01 ^a	0.21 \pm 0.01 ^b
N,PP	0.58 \pm 0.02 ^b	0.08 \pm 0.01 ^a	0.32 \pm 0.02 ^a
NN,PP	0.66 \pm 0.02 ^a	0.12 \pm 0.01 ^a	0.21 \pm 0.01 ^b
<i>F</i> – value (df 3,16)	9.09 ^{**}	0.88 ^{NS}	16.64 ^{**}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Significant difference ($p < 0.01$); ^{*} significant difference ($p < 0.05$); ^{NS} non-significant difference ($p > 0.05$).

Table 6. *Panicum hemitomom* root:shoot ratio and root volume (cm³) for the phase – II study (Chapter 2). Values are means \pm SE (n = 5).

<u>Saturated treatments</u>		
Nutrient regime	Root:shoot ratio	Root volume (cm ³)
N,P	1.1 \pm 0.15 ^b	50.3 \pm 17.83 ^{ba}
NN,P	2.1 \pm 0.18 ^{ba}	91.3 \pm 4.34 ^a
N,PP	1.16 \pm 0.09 ^{ba}	64.8 \pm 15.02 ^b
NN,PP	2.1 \pm 0.35 ^a	131.6 \pm 19.21 ^a
<i>F</i> – value (df 3,16)	6.69 ^{**}	5.48 ^{**}
<u>Inundated treatments</u>		
Nutrient regime	Root:shoot ratio	Root volume (cm ³)
N,P	1.4 \pm 0.14 ^b	22.5 \pm 10.51 ^a
NN,P	3.2 \pm 0.31 ^a	28.2 \pm 15.49 ^a
N,PP	1.84 \pm 0.22 ^b	12.1 \pm 1.59 ^a
NN,PP	3.2 \pm 0.40 ^a	17.1 \pm 1.16 ^a
<i>F</i> – value (df 3,16)	10.72 ^{**}	0.54 ^{NS}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Significant difference ($p < 0.01$); ^{NS} non-significant difference ($p > 0.05$).

Table 7. *Panicum hemitomom* mean root diameter (cm), length (cm), volume (cm³), and number of tips (#) for the phase – II study (Chapter 2). Values are means \pm SE (n = 20).

<u>Saturated treatments</u>				
Nutrient regime	Diameter (cm ³)	Length (cm)	Volume (cm ³)	Number of tips (#)
N,P	0.43 \pm 0.024 ^a	303.2 \pm 47.23 ^a	0.37 \pm 0.060 ^{ba}	1169.7 \pm 182.3 ^a
NN,P	0.46 \pm 0.014 ^a	240.9 \pm 20.14 ^a	0.43 \pm 0.038 ^a	872.6 \pm 70.05 ^a
N,PP	0.44 \pm 0.019 ^a	329.7 \pm 31.89 ^a	0.46 \pm 0.032 ^b	1250.4 \pm 138.7 ^a
NN,PP	0.46 \pm 0.008 ^a	250.2 \pm 24.47 ^a	0.41 \pm 0.037 ^a	950.7 \pm 96.6 ^a
<i>F</i> – value (df 3,76)	0.83 ^{NS}	1.70 ^{NS}	0.73 ^{NS}	1.91 ^{NS}

<u>Inundated treatments</u>				
Nutrient regime	Diameter (cm ³)	Length (cm)	Volume (cm ³)	Number of tips (#)
N,P	0.50 \pm 0.044 ^a	119.4 \pm 37.96 ^a	0.17 \pm 0.044 ^a	352.0 \pm 87.8 ^a
NN,P	0.45 \pm 0.019 ^a	71.22 \pm 12.88 ^a	0.09 \pm 0.013 ^{ba}	290.2 \pm 61.4 ^a
N,PP	0.53 \pm 0.022 ^a	43.62 \pm 6.17 ^a	0.08 \pm 0.005 ^b	197.1 \pm 23.4 ^a
NN,PP	0.49 \pm 0.020 ^a	58.57 \pm 8.26 ^a	0.09 \pm 0.010 ^{ba}	201.5 \pm 23.4 ^a
<i>F</i> – value (df 3,76)	1.35 ^{NS}	2.51 ^{NS}	2.86 [*]	1.77 ^{NS}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{*} Significant difference ($p < 0.05$); ^{NS} non-significant difference ($p > 0.05$).

Table 8. The effect of manipulated nutrient availability and hydrology on the proportion of *Panicum hemitomon* total root length per root diameter class for the phase – II study (Chapter 2). All measurements were performed on live root tissue sampled immediately prior to experimental harvest (after four months of growth). Values are means \pm SE (n = 5).

Treatment	Root diameter classes (mm)				
	0.0 – 0.49	0.5 – 0.99	1.0 – 1.49	1.5 – 1.99	2.0 – 4.99
N,P (s)	0.80 \pm .033 ^a	0.05 \pm .028 ^a	0.12 \pm .019 ^{ba}	0.03 \pm .010 ^{dc}	-----
N,P (i)	0.72 \pm .035 ^a	0.09 \pm .021 ^{ba}	0.15 \pm .037 ^{ba}	0.03 \pm .008 ^{bdac}	-----
NN,P (s)	0.80 \pm .017 ^a	0.04 \pm .008 ^{ba}	0.08 \pm .019 ^b	0.08 \pm .012 ^a	-----
NN,P (i)	0.74 \pm .014 ^a	0.09 \pm .012 ^{ba}	0.15 \pm .008 ^{ba}	0.02 \pm .005 ^d	-----
N,PP (s)	0.81 \pm .022 ^a	0.02 \pm .005 ^b	0.08 \pm .018 ^b	0.07 \pm .004 ^{ba}	0.01 \pm .001
N,PP (i)	0.70 \pm .033 ^a	0.05 \pm .009 ^{ba}	0.21 \pm .034 ^a	0.03 \pm .009 ^{bdc}	0.01 \pm .001
NN,PP (s)	0.79 \pm .014 ^a	0.04 \pm .005 ^{ba}	0.10 \pm .024 ^b	0.06 \pm .013 ^{bac}	0.01 \pm .001
NN,PP (i)	0.72 \pm .032 ^a	0.10 \pm .014 ^{ba}	0.16 \pm .028 ^{ba}	0.02 \pm .005 ^{dc}	-----
<i>F</i> – value					
(df 7,32)	2.80 [*]	3.59 [*]	3.18 [*]	6.00 ^{**}	NA

^a Means with the same letter in the same column are not statistically different (p < 0.05) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference (p < 0.01); ^{*} significant difference (p < 0.05).

Table 9. The effect of manipulated nutrient availability and hydrology on the proportion of *Panicum hemitomon* total root volume per root diameter class for the phase – II study (Chapter 2). All measurements were performed on live root tissue sampled immediately prior to experimental harvest (after four months of growth). Values are means \pm SE (n = 5)

Treatment	Root diameter classes (mm)				
	0.0 – 0.49	0.5 – 0.99	1.0 – 1.49	1.5 – 1.99	2.0 – 4.99
N,P (s)	0.08 \pm .006 ^a	0.10 \pm .028 ^a	0.55 \pm .085 ^{ba}	0.21 \pm .069 ^{dc}	0.06 \pm .000
N,P (i)	0.07 \pm .012 ^a	0.13 \pm .040 ^{ba}	0.50 \pm .095 ^{ba}	0.20 \pm .061 ^{bdac}	0.10 \pm .000
NN,P (s)	0.08 \pm .010 ^a	0.04 \pm .014 ^{ba}	0.35 \pm .056 ^b	0.44 \pm .076 ^a	0.09 \pm .003
NN,P (i)	0.08 \pm .006 ^a	0.14 \pm .017 ^{ba}	0.57 \pm .048 ^{ba}	0.13 \pm .036 ^d	0.08 \pm .000
N,PP (s)	0.06 \pm .007 ^a	0.02 \pm .003 ^b	0.33 \pm .049 ^b	0.46 \pm .054 ^{ba}	0.11 \pm .000
N,PP (i)	0.06 \pm .012 ^a	0.09 \pm .027 ^{ba}	0.62 \pm .055 ^a	0.16 \pm .041 ^{bdc}	0.07 \pm .000
NN,PP (s)	0.07 \pm .005 ^a	0.04 \pm .004 ^{ba}	0.40 \pm .109 ^b	0.38 \pm .071 ^{bac}	0.11 \pm .019
NN,PP (i)	0.08 \pm .017 ^a	0.14 \pm .022 ^{ba}	0.53 \pm .054 ^{ba}	0.18 \pm .027 ^{dc}	0.07 \pm .025
<i>F</i> – value (df 7,32)	0.57 ^{NS}	2.78 [*]	2.08 ^{NS}	5.41 ^{**}	NA

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference ($p < 0.01$); ^{*} significant difference ($p < 0.05$); ^{NS} non-significant difference ($p > 0.05$).

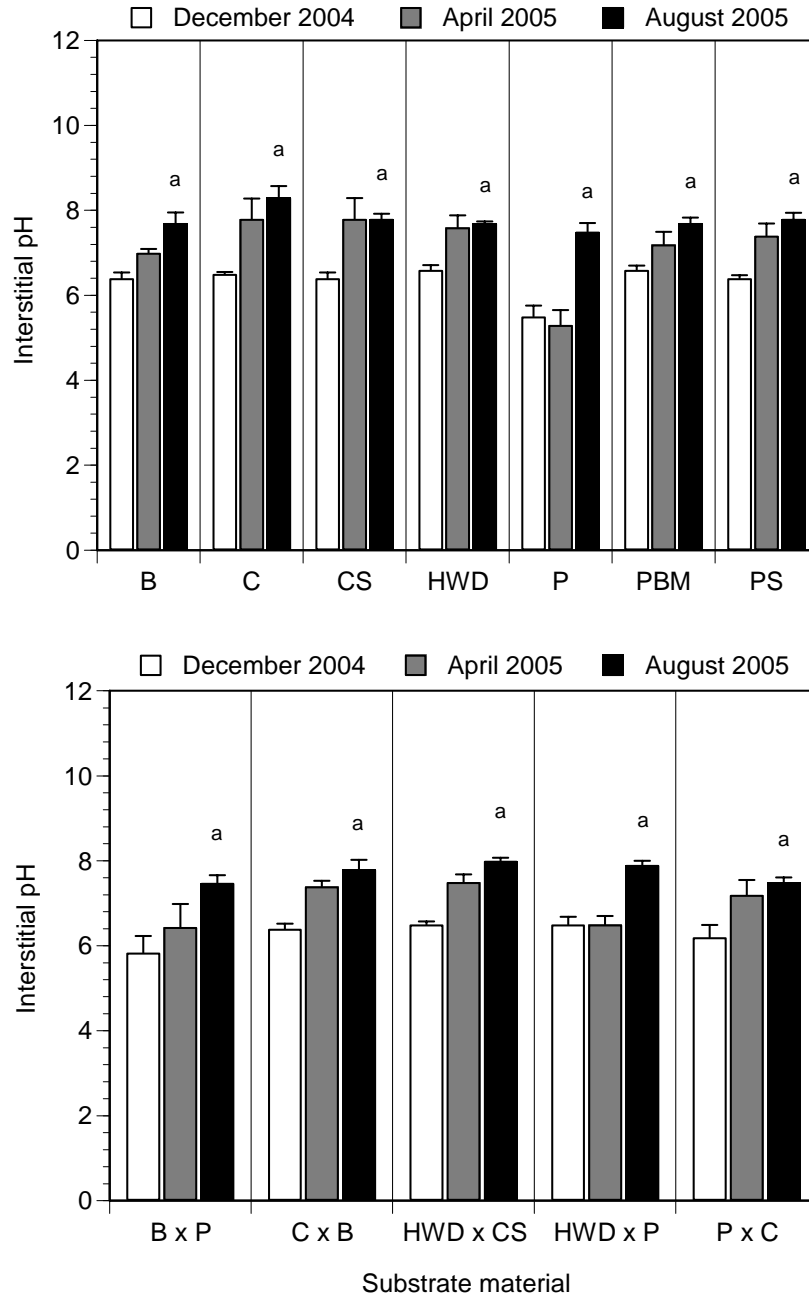


Figure 3. The effect of individual (top panel) and blended (bottom panel) substrate material on interstitial pH for experiment – 1 (Chapter 3). Treatment codes are as follows: B = bagsse; C = cypress mulch; CS = sugarcane leaf strippings; HWD = hardwood mulch; P = peat; PBM = pine bark mulch; PS = pine shavings; B x P = bagasse and peat; C x B = cypress mulch and bagasse; HWD by CS = hardwood mulch and sugarcane leaf strippings; HWD x P = hardwood mulch and peat; P x C = peat and cypress mulch. Values are means \pm SE (n = 5). Statistical significance is as follows: time (Wilks' Lambda: $F_{5,44} = 256.71$, $p < 0.0001$); time by substrate material (Pillai's Trace: $F_{55,240} = 2.59$, $p < 0.0001$). Letters over bars represent significantly different means for August 2005 data only (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{11,48} = 1.76$, $p = 0.0811$).

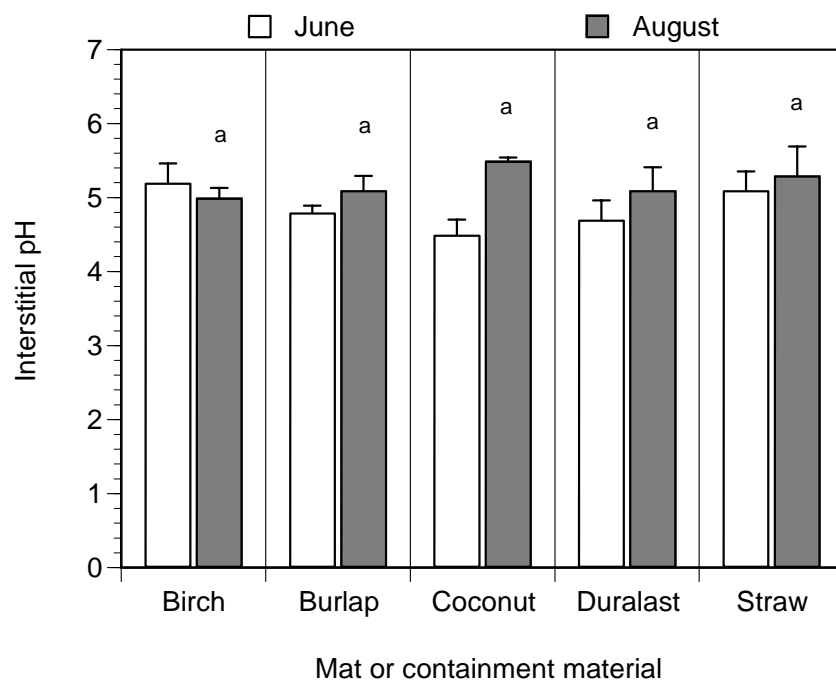


Figure 4. The effect of mat or containment material and peat substrate on interstitial pH for experiment – 2 (Chapter 3). Values are means \pm SE ($n = 5$). Statistical significance is as follows: time (Wilks' Lambda: $F_{1,20} = 5.81$, $p = 0.0257$); time by mat material (Wilks' Lambda: $F_{4,20} = 1.58$, $p = 0.2190$). Letters over bars represent significantly different means for August data only (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{4,20} = 0.62$, $p = 0.6517$).

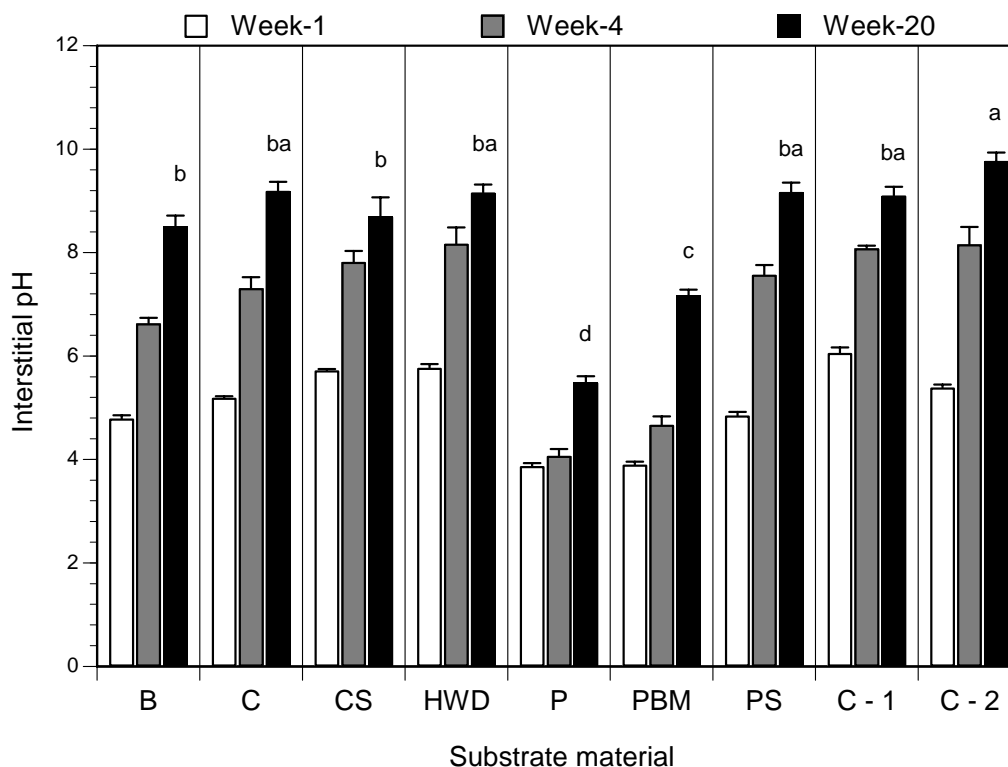


Figure 5. The effect of substrate material on interstitial pH for experiment – 3 (Chapter 3). Treatment codes are as follows: B = bagsse; C = cypress mulch; CS = sugarcane leaf strippings; HWD = hardwood mulch; P = peat; PBM = pine bark mulch; PS = pine shavings; C – 1 = tap water; C – 2 = tap water by Duralast coconut fiber. Values are means \pm SE (n = 5). Statistical significance is as follows: time (Wilks' Lambda: $F_{2,35} = 1757.93$, $p < 0.0001$); time by treatment (Pillai's Trace: $F_{16,72} = 7.53$, $p < 0.0001$). Letters over bars represent significantly different means for week-20 data only (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{8,36} = 45.45$, $p < 0.0001$).

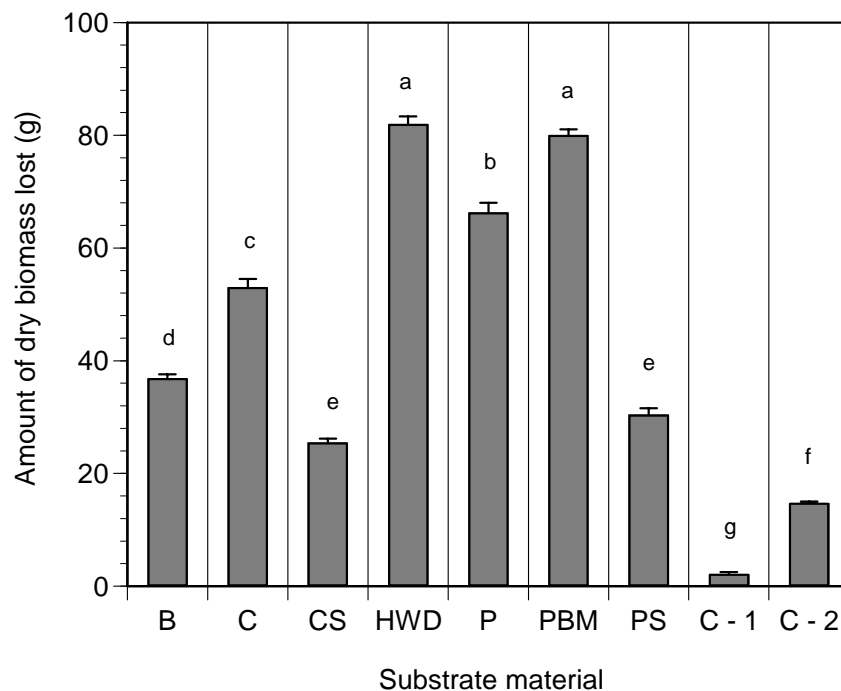


Figure 6. The amount of biomass lost to decomposition for experiment – 3 (Chapter 3). Treatment codes are as follows: B = bagsse; C = cypress mulch; CS = sugarcane leaf strippings; HWD = hardwood mulch; P = peat; PBM = pine bark mulch; PS = pine shavings; C – 1 = tap water; C – 2 = tap water by Duralast coconut fiber. Values are means \pm SE ($n = 5$). Letters over bars represent significantly different means (Tukey's pairwise comparisons, $\alpha = 0.05$; $F_{8,36} = 725.98$, $p < 0.0001$).

Table 10. The effect of substrate material on *Panicum hemitomom* tissue nitrogen content (5), net CO₂ assimilation ($\mu\text{mol C m}^{-2} \text{ s}^{-1}$), and PNUE ($\mu\text{mol C g}^{-1} \text{ N s}^{-1}$) for experiment – 1 (Chapter 3). Values are means \pm SE (n = 5).

Substrate material	Tissue nitrogen content (%)	Net CO ₂ assimilation ($\mu\text{mol C m}^{-2} \text{ s}^{-1}$)	PNUE ($\mu\text{mol C g}^{-1} \text{ N s}^{-1}$)
Bagasse	1.63 \pm 0.11 ^a	12.73 \pm 1.35 ^a	40.0 \pm 3.1 ^a
Cypress mulch	1.75 \pm 0.07 ^a	17.59 \pm 2.68 ^a	16.41 \pm 2.34 ^a
Sugarcane leaf strippings	1.52 \pm 0.13 ^a	13.51 \pm 2.66 ^a	14.27 \pm 2.07 ^a
Hardwood mulch	1.47 \pm 0.13 ^a	14.95 \pm 2.00 ^a	16.49 \pm 1.05 ^a
Peat	1.19 \pm 0.12 ^a	12.58 \pm 1.45 ^a	17.48 \pm 1.99 ^a
Pine bark mulch	1.53 \pm 0.10 ^a	19.05 \pm 3.28 ^a	20.3 \pm 3.01 ^a
Pine shavings	1.47 \pm 0.12 ^a	13.57 \pm 3.41 ^a	14.74 \pm 3.34 ^a
Bagasse and Peat	1.52 \pm 0.17 ^a	15.89 \pm 3.52 ^a	16.66 \pm 3.14 ^a
Cypress mulch and Bagasse	1.53 \pm 0.03 ^a	12.88 \pm 2.77 ^a	13.62 \pm 2.77 ^e
Hardwood mulch and Sugarcane leaf strippings	1.34 \pm 0.10 ^a	13.87 \pm 1.64 ^a	16.65 \pm 1.31 ^a
Hardwood mulch and Peat	1.37 \pm 0.07 ^a	16.62 \pm 2.53 ^a	20.54 \pm 4.04 ^a
Peat and Cypress mulch	1.40 \pm 0.16 ^a	17.49 \pm 1.62 ^a	21.29 \pm 2.96 ^a
<i>F</i> – value (df 11,48)	1.38 ^{NS}	0.77 ^{NS}	1.05 ^{NS}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference ($p < 0.01$).

Table 11. The effect of substrate material on *Panicum hemitomom* total stem number, total stem height (cm), and mean stem height (cm) for experiment – 1 (Chapter 3), all measured at harvest after nine months of growth. Values are means \pm SE (n = 5).

Substrate material	Total stem number (#)	Total stem height (cm)	Mean stem height (cm)
Bagasse	25.0 \pm 5.2 ^d	970.2 \pm 198.3 ^c	40.0 \pm 3.1 ^{ebdc}
Cypress mulch	24.8 \pm 5.8 ^d	954.14 \pm 211.9 ^d	39.2 \pm 2.6 ^{edc}
Sugarcane leaf strippings	54.0 \pm 10.7 ^{bdac}	2730.7 \pm 598.5 ^{bac}	49.0 \pm 3.6 ^{bdac}
Hardwood mulch	40.4 \pm 2.9 ^{bdc}	1728.9 \pm 172.3 ^{bc}	42.6 \pm 1.6 ^{ebdac}
Peat	74.8 \pm 3.5 ^{ba}	4010.7 \pm 146.2 ^{ba}	53.8 \pm 1.6 ^a
Pine bark mulch	68.2 \pm 9.1 ^{bac}	3177.2 \pm 605.6 ^{bac}	45.5 \pm 2.6 ^{ebdac}
Pine shavings	41.0 \pm 16.4 ^{bdc}	1858.3 \pm 1077.4 ^{bc}	36.8 \pm 5.4 ^{ed}
Bagasse and Peat	84.0 \pm 14.7 ^a	4663.7 \pm 1006.0 ^a	54.4 \pm 2.0 ^a
Cypress mulch and Bagasse	27.8 \pm 2.9 ^{dc}	963.1 \pm 140.7 ^c	34.0 \pm 1.8 ^e
Hardwood mulch and Sugarcane leaf strippings	64.6 \pm 10.8 ^{bdac}	3189.0 \pm 532.4 ^{bac}	49.3 \pm 1.3 ^{bdac}
Hardwood mulch and Peat	60.0 \pm 3.8 ^{bdac}	3158.7 \pm 169.7 ^{bac}	52.8 \pm 1.1 ^{bac}
Peat and Cypress mulch	76.6 \pm 2.4 ^{ba}	4095.5 \pm 168.2 ^{ba}	53.5 \pm 1.9 ^{ba}
<i>F</i> – value (df 11,48)	5.88 ^{**}	6.06 ^{**}	7.27 ^{**}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference ($p < 0.01$).

Table 12. The effect of mat or containment material on Panicum hemitomom total stem number, total stem height (cm), and mean stem height (cm) for experiment – 2 (Chapter 3), all measured at harvest after three months of growth. Values are means \pm SE (n = 5).

Mat or containment material	Total stem number (#)	Total stem height (cm)	Mean stem height (cm)
Birch	15.4 \pm 1.63 ^c	457.2 \pm 43.43 ^c	29.9 \pm 1.29 ^b
Burlap	34.2 \pm 2.51 ^a	1177.0 \pm 48.62 ^a	34.7 \pm 1.07 ^a
Coconut	28.4 \pm 2.65 ^{ba}	1044.1 \pm 69.84 ^{ba}	37.1 \pm 1.14 ^a
Duralast	24.6 \pm 1.40 ^{bc}	908.34 \pm 53.67 ^b	36.9 \pm 0.68 ^a
Straw	23.2 \pm 2.57 ^{bc}	784.2 \pm 87.77 ^b	33.9 \pm 1.15 ^{ba}
<i>F</i> – value (df 4,20)	9.71 ^{**}	19.26 ^{**}	7.12 ^{**}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Highly significant difference ($p < 0.01$).

Table 13. Proportional contributions of *Panicum hemitomon* stem and leaf, rhizome, and root biomass to total biomass based on dry biomass totals for each multi-species treatment (Chapter 4), obtained after five months of growth. Values are means \pm SE (n = 5).

Treatment	Shoot contribution	Rhizome contribution	Root contribuion
Ph	0.37 \pm 0.051 ^a	0.33 \pm 0.010 ^a	0.28 \pm 0.052 ^a
PhAp	0.34 \pm 0.011 ^a	0.29 \pm 0.019 ^{ba}	0.35 \pm 0.008 ^a
PhHr	0.35 \pm 0.001 ^a	0.30 \pm 0.012 ^{ba}	0.33 \pm 0.011 ^a
PhLp	0.38 \pm 0.010 ^a	0.24 \pm 0.007 ^b	0.37 \pm 0.006 ^a
PhSl	0.32 \pm 0.014 ^a	0.33 \pm 0.019 ^a	0.34 \pm 0.032 ^a
Ph all	0.34 \pm 0.026 ^a	0.29 \pm 0.014 ^{ba}	0.36 \pm 0.016 ^a
Ph edge	0.34 \pm 0.014 ^a	0.30 \pm 0.012 ^a	0.35 \pm 0.007 ^a
<i>F</i> – value (df 6,21)	0.74 ^{NS}	4.91 ^{**}	1.44 ^{NS}

^a Means with the same letter in the same column are not statistically different ($p < 0.05$) based on Tukey's multiple comparison procedure for all possible pairwise comparisons. ^{**} Significant difference ($p < 0.01$); ^{NS} non-significant difference ($p > 0.05$).

Vita

Charles Ellery Mayence, son of Charles Roger Mayence and Sarah Francis Horrmann, was born in Pensacola, Florida on the eighth day of December, 1975. Ellery's current interest in natural resource ecology arose out of a childhood that was in many ways defined not only by nature itself, but by an interest to become more knowledgeable of the environment of which he is an integral part. Whether it was fishing and swimming in the Gulf of Mexico and neighboring wetlands along the Florida Panhandle, or camping and fishing in the Appalachian Mountains of western North Carolina, Ellery developed a desire at an early age to be outside rather than in. This desire continues to define Ellery's persona today. Ellery graduated from Orange High School in Hillsborough, North Carolina in 1993 and returned to Florida for three years to begin college. In all reality, significantly more time was spent fishing, and school quickly became a distant concern. However, with maturity, Ellery learned the value of an education, and began his pursuit anew. After a short stint at Pensacola Junior College, Ellery transferred to the University of North Carolina at Chapel Hill, where in 1999 he graduated (with highest honors and highest distinction) with BA in Geography and a minor in Geology. Ellery then spent two years traveling and working miscellaneous jobs before being accepted into the Master of Environmental Management program at the Nicholas School of the Environment and Earth Sciences at Duke University. Immediately after classes began in 2001, Ellery married Kasia Krzysztoforska, very special woman whom he befriended several years prior. Ellery's educational experience at Duke University was exceptionally positive, opening doors on many academic and professional fronts. After graduating in 2003 with a Masters of Environmental Management in Resource Ecology, Ellery and Kasia relocated to New Orleans, where he began his doctoral studies in Conservation Biology at the University of New Orleans. Ellery was offered a research assistantship in the Coastal Plant Sciences Laboratory in the Department of

Biological Sciences. Dr. Mark Hester, the laboratory director, agreed to serve as his academic advisor, and a lasting friendship quickly developed. While at the University of New Orleans under the guidance of Dr. Mark Hester, Ellery received numerous merit-based awards and research grants including a prestigious EPA Science to Achieve Results (STAR) Fellowship, a commendable accomplishment that further enhanced his doctoral studies. Ellery's doctoral studies were focused on elucidating Panicum hemitomom (maidencane) growth responses with respect to developing a preliminary design for restoring thick-mat floating marsh. Ellery anticipates receiving his Ph.D in December of 2007, and plans to transition into a career in applied ecological restoration.