ENVIRONMENTAL FACTORS AND *TYPHA* SPP. DOMINANCE IN CREATED WETLANDS

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TABLE OF CONTENTS

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LIST OF TABLES

LIST OF FIGURES

Abstract

As created wetlands are becoming more common due to compensatory mitigation under section 404 of the Clean Water Act, it has become important to understand how the vegetation community and the soil nutrient availability develop over time. For a created wetland to replace the function of the destroyed natural wetland, the biogeochemical cycling and vegetation community must replicate the natural system. In this study, I sampled the vegetation community as well as the soil and porewater nutrient availability in four created wetlands in southeastern Virginia, constructed and managed by the Virginia Department of Transportation. All the sites used in this study had areas of dense *Typha* spp. stands, which had been identified as problem areas by the site managers,based on inferences from previous research indicating *Typha* are invasive in other types of wetlands. In many of these sites, the *Typha* populations were removed by cutting and herbicide spraying, due to the assumption that the dense *Typha* stands hinder the biodiversity and therefore reduce the functionality of the created wetlands. As part of this study, I sampled the composition of the vegetation community both within *Typha* stands and in areas dominated by other species. I was able to show that the dense *Typha* stands do not lower the species richness or the Shannon diversity index of the vegetation community. I also measured the nutrient availability associated with *Typha* stands and areas dominated by other vegetation and found no consistent significant differences in soil nutrient availability. However, I did observe a change in nutrient concentration across all vegetation communities and in all study sites from 2006 to 2007. The soil a range of 20 and 55 in 2007. These results may indicate that as created wetlands mature the amount of soil total phosphorus (TP) decreases and the amount of total nitrogen (TN) increases, resulting in a steady state of P limitation relative to N as the site matures. Since these conclusions are based on only two years of data, longer-term research is needed in created wetlands to verify trends in soil TP and TN dynamics as these sites mature.

ENVIRONMENTAL FACTORS AND *TYPHA* SPP. DOMINANCE IN CREATED WETLANDS

INTRODUCTION

Wetland creation is the process of converting a system that was previously upland or shallow water into a wetland (Mitsch and Gosselink 2000). Wetlands are created for a variety of purposes, including wastewater treatment, wildlife habitat, retention of drainage water, and most often to mitigate destruction of natural wetlands. The creation of wetlands for mitigation is due, in part, to the permitting process that is required under section 404 of the Clean Water Act (CWA) (33 U.S.C. s/s 1251 et seq.) passed in 1977; section 404 regulates dredge and fill activities in the nation's waters. In certain cases, such as in the construction of roads, wetland loss is determined to be unavoidable, and therefore, the destruction of natural wetlands must be mitigated by restoring or creating a wetland of the same type. However, it has been shown that wetlands created to fulfill the requirements of section 404, often fail to replace the function and structure of the wetland that was destroyed (Zedler 1996). This is a pressing concern because the regulations that are designed to limit the loss of wetland ecosystems may be facilitating the loss of many of the functions provided by wetlands, such as nutrient and sediment removal, flood remediation, and protection of habitat and biodiversity. Therefore, more studies need to be conducted to investigate the degree to which created wetlands are able to replicate the structure and function of the systems they are meant to replace.

One of the most common causes of failure to replicate desired structure and function in created wetlands is invasion by undesirable nuisance plant species such as

Typha , *Phragmites australis* (Cav.) Trin. ex Steud., and *Lythrum salicaria* L. These species are all considered to be invasive in some types of wetlands (Weihe and Neely 1997, Galatowitsch et al. 1999, Zedler and Kercher 2004). Invasion is often associated with disturbances to the system particularly from changes in nutrient availabilities, hydrology, and salinity (Galatowitsch et al. 1999, Ellstrand and Schierenbeck 2006, Woo and Zedler 2002). The disturbances associated with wetland creation have also been linked to invasion by nuisance plant species, particularly *Typha* spp. and *P. australis*. Both of these species are large perennial species, that are able to reproduce very quickly by clonal and propagule distribution. These traits allow them to effectively outcompete other colonizers and form dense monospecific stands on the open substrate that is available in newly created wetlands.

This research will focus primarily on the role of *Typha* spp. (cattails) in the vegetation community development of created wetlands located in the Coastal Plain physiographic province of Virginia, and will investigate the influence of environmental characteristics, such as hydrology, soil physical and chemical parameters, and nutrient availability, on the vegetation development in these systems. I particularly wanted to investigate the role of soil biogeochemistry in the dominance of *Typha* in these systems. Dense stands of *Typha* in these sites are generally considered by site managers to indicate that the vegetation community has not replicated the structure of a natural system (pers. comm. VA Department of Transportation). The inability to achieve the desired plant community may indicate that there are other aspects of the site design that are not functionally correct. The vegetation community is responding to the soil and nutrient environment in which they find themselves, and are only able to persist as long as the environmental conditions that support them are present. The common management response to a perceived monoculture of *Typha* or *P. australis* is cutting and/or spraying the site with herbicide. While this does change the structure of the vegetation community for a period of time after treatment, the nuisance vegetation often comes back and dominates the system within a few years. Removal of the vegetation does not address the underlying issues, that these sites may not have the correct soil and biogeochemical environment to support the desired vegetation community. Therefore, the environmental conditions and competitive adaptations that facilitate *Typha* invasion into created mitigation wetlands are the focus of this research project; particularly the relationships between the time since construction, nutrient availability, and nutrient uptake by *Typha*. While invasiveness has been observed for multiple species in the family Typhaceae (Thieret and Luken 1996), this project will focus on *Typha latifolia* L., T*ypha angustifolia* L., and the hybrid between the two, *Typha* x *glauca* Godr., these are the three species most common in the Coastal Plain region of Virginia.

Despite problems with the implementation of wetland mitigation, it is a practice that is becoming more and more common and will continue to be used in the future. As a result of this, it is especially important to learn as much as possible about what is controlling the successional development of these sites, and the biogeochemical processes taking place in the soil. With increased knowledge, created wetlands will have a much better chance of maturing into functionally equivalent systems. By determining the role of biogeochemistry in controlling the vegetation community that persists in created wetlands, I hoped to provide background to help site managers and designers create sites that are both functionally and structurally equivalent to natural systems.

Chapter 1: Literature Review

The Wetland Environment

Various environmental factors facilitate the existence of wetlands in the landscape including regional climate, geomorphology, hydrology, and biogeochemistry. The specific type of wetland that exists at a given location is dependent on the occurrence of a relatively narrow range of environmental variables (Mitsch and Gosselink 2000). Latitude and regional geomorphic features determine the climatic conditions. Climate in turn exerts control on the vegetation of a site through influences on hydrology (the amount of precipitation and evapotranspiration), temperature range of both air and soil, and the amount of photosynthetically active radiation (PAR) that reaches the canopy. In herbaceous wetlands, the lack of shading allows for very high levels of PAR to reach the emergent vegetation. Geologic conditions that influence wetlands include: surface relief, slope, permeability of the soil, geochemical controls, as well as the hydrologic properties of the underlying strata (Bedford 1996). Climate, geomorphology, hydrology, and the connections between them have a strong influence on the zonation and succession of hydrophytic plant communities in wetland ecosystems.

Wetlands are often defined by the dominant inflows of water, these include groundwater, precipitation, and surface flow. Some of the associated hydrologic designations include tidal or non-tidal influence, riverine, palustrine, and lacustrine

(Cowardin et al. 1979). The hydroperiod is the seasonal pattern of water level fluctuation unique to every system, which is controlled by the water budget (inflows and outflows) and physical aspects of the surrounding environment, such as soil permeability and proximity to other water bodies (Mitsch and Gosselink 2000). The hydroperiod determines the amount of time the wetland is inundated during the year, and directly modifies the physiochemical factors of the system such as, soil composition, reduction oxidation (redox) potential, and nutrient availability.

Biogeochemistry

Soil development in wetlands is governed by a variety of processes including, physical and chemical weathering, organic matter incorporation, and the amount of available oxygen, which controls the redox potential of the soil environment. Hydric soils vary from upland soils because of the unique biogeochemical reactions that occur under saturated conditions. Inundation, or saturation of the soil surface, replaces the air that is normally found in the pore spaces with water (Mausbach and Richardson 1994). The diffusion of molecular oxygen through water is 10,000 times slower than through air. Therefore, as oxygen in the water is depleted through use as a terminal electron acceptor in microbial respiration, oxygen replenishment, through molecular diffusion, is not able to keep up and hypoxic or anoxic conditions develop (Hale and Orcutt 1987, Mitsch and Gosselink 2000). Anoxic conditions in the soil profile are a common characteristic of wetland systems. The amount of available oxygen is an important controlling factor in the development of hydric soils, as well as an important influence on the cycling and availability of nutrients within the system. The chemical progression of soils from an oxidized state to a reduced state can be observed through measurements of the redox potential, a measure of the electron pressure or availability in a solution, that is reported in millivolts (mV) (Mitsch and Gosselink 2000). As alternate electron acceptors are used, a continual lowering of the redox potential occurs. The lowering of the redox potential continues as the period of time the soil is inundated increases. If the water level falls and the soil is able to come back into contact with atmospheric oxygen the redox potential increases (Cronk and Fennessey 2001).

Following inundation and lowering of the redox potential, a series of microbially mediated redox reactions take place in wetland sediments. The hierarchy of redox reactions in which compounds other than oxygen are used as terminal electron acceptors for microbial respiration can be seen in Table 1. The first suite of reactions theoretically occurs at 250 mV and includes a series of redox reactions called denitrification. Denitrification results in the formation of nitrogen gas (N_2) and a loss of labile nitrogen from the system. This process involves the reduction of nitrate (NO_3^-) to nitrous oxide (N_2O), and finally to nitrogen gas (N_2), which is not a bioavailable form and is lost to atmospheric diffusion (Mitsch and Gosselink 2000, Smith and Smith 2001).

Manganese and iron reduction are the next reactions to occur following the depletion of NO_3^- as an electron acceptor. Manganese reduction occurs at a theoretical redox potential of about 225 mV and is a microbially mediated process. Iron reduction, both microbially and chemically mediated, occurs at a redox potential of 120 mV (Cronk and Fennessey 2001). Both iron and manganese have a conspicuous oxidized precipitate form, which can be clearly seen in oxidized soils. Manganic oxy-hydroxide is black, and ferric oxy-hydroxide is a reddish-orange color. The reduced forms of both minerals are soluble in water. The dissolution of iron and manganese under reduced conditions results in exposure of the bluish gray background matrix color of gleyed soil.

Table 1: The oxidized and reduced forms of major elements and the theoretical, pH 7.0 adjusted, redox potential at which reduction reactions begin to occur, as well as the effects the reductions have on the surrounding vegetation (adapted from Cronk and Fennessey, 2001).

Element	Oxidized Form	Reduced Form	Adjusted Redox Potential (pH 7) (mV)	Effects on Vegetation
Nitrogen	NO_3^-	N_2O, N_2	250	Denitrification removes labile N from the soil through loss to atmosphere
Manganese	Mn^{+4}	Mn^{+2}	225	High levels of reduced Mn can interfere with enzyme structure and nutrient composition
Iron	Fe^{+3}	Fe^{+2}	120	High levels of reduced Fe can interfere with Mg during chlorophyll formation; causing discolored leaves, diminished photosynthesis, and decreased root respiration
Sulfur	SO_4^{-2}	S^{-2}, HS^-, H_2S	-75 to -150	Inhibits photosynthesis and the ability of the roots to respire aerobically and anaerobically
Carbon	CO_2	CH_4	-250 to -350	Has no effect on plants, is merely transported through gas spaces and released to the atmosphere

The reduction of sulfate to sulfide occurs at a redox potential of between -75 and -150 mV. Sulfate is much more abundant in sea water than in freshwater, therefore salt marshes have much higher concentrations of sulfides than freshwater wetlands (Cronk and Fennessey 2001). Sulfur reduction produces hydrogen sulfide that is released to the atmosphere, resulting in a loss of bioavailable sulfur to the system.

Methanogenesis and fermentation also occur low on the redox hierarchy; both processes use carbon as the terminal electron acceptor; methanogenesis uses CO_2 and fermentation uses simple low molecular weight organic compounds. The methane that is formed is not retained in the plants or the soils; instead, it diffuses from the root zone, through the pore spaces, and back to the atmosphere (Mitsch and Gosselink, 2000, Cronk and Fennessey, 2001).

The redox potential of wetland soil has a large impact on nutrientions that are directly transformed by changes in redox conditions, as well as nutrients that do not undergo redox reactions. This is especially important for phosphorus (P) availability, which is greatly increased in reduced conditions, even though phosphate ions do not undergo redox reactions. This is because orthophosphates form complexes with ferric oxyhydroxides under oxidizing conditions, which are released as soils reduce. P is an important limiting nutrient in many ecosystems, including freshwater marshes and southern deepwater swamps (Mitsch and Gosselink 2000). It occurs as inorganic and organic soluble forms, as well as in particulate organic matter and in microbial biomass (Table 2) and has no gas phase, occurring only in a sedimentary cycle. In general only dissolved inorganic phosphorus is considered biologically available (Mitsch and Gosselink 2000).

As mentioned above, phosphorus does not directly undergo redox reactions, however its availability is heavily influence by the chemical conditions of the surrounding water and soil. Available phosphorus can be removed from the system by adsorption to clay particles and organic peat, as well as by microbial and plant uptake. Under aerobic conditions, it can adsorb to and form precipitates with iron and aluminum oxyhydroxides. Under anaerobic conditions, dissolution of ferric oxide releases inorganic soluble phosphorus, leading to higher availability of orthophosphates under reduced conditions (Cronk and Fennessey 2001). The soil pH can also be an important factor in controlling the availability of phosphorus. In acid soils, phosphorus is generally precipitated and fixed as aluminum and iron phosphates; in alkaline soils, phosphorus is bound by calcium and magnesium. These processes result in lower bioavailable phosphorus in both types of soils. Phosphorus is most bioavailable in neutral to slightly acidic soils (Reddy et al. 1999, Mitsch and Gosselink 2000).

Table 2: Common organic and inorganic forms of phosphorus (from Mitsch and Gosselink 2000).

Phosphorus	Soluble Forms	Insoluble Forms
Inorganic	• Orthophosphates ($H_2PO_4^- HPO_4^{2-}$, PO_4^{3-})	• Clay-phosphate complexes • Metal hydroxide phosphates, such as, vivianite $Fe_3(PO_4)_2$, variscite $Al(OH)_2H_2PO_4$ • Minerals, such as, apatite $[Ca_{10}(OH)_2(PO_4)_6]$
Organic	• Dissolved organics, such as inositol phosphates, phospholipids, phosphoproteins	• Organic phosphorus bound to organic matter • Active microbial biomass

Hydric Soils

Hydric soils are defined as a soil that is formed under conditions of saturation, flooding or ponding long enough during the growing season to develop anaerobic conditions in the upper part (Federal Register 1994). One of these defining characteristics is the distinct grayish color of many hydric soils, which forms when inundation and lowering of the redox potential leads to the reduction of iron and manganese. As the reduced forms of iron and manganese leach out of the soil, the background color of the soil's mineral matrix can be seen, usually gray or bluish-gray. This process is called gleization, and is a distinguishing characteristic of hydric soils

(USACoE 1987, Mitsch and Gosselink 2000). When there are fluctuations in the water table, nodules of precipitated iron (reddish) and manganese (black) oxides can often be seen at or above the saturation horizon, where they formed during periods of oxidation. These distinctly colored mottles, called redoximorphic features, are another characteristic used to define hydric soils (USACoE 1987).

Another type of redoximorphic feature is created by the process of radial oxygen loss, in which the soil surrounding the roots of hydrophytic plants can become saturated with oxygen due to the release of oxygen from the root sheaths (Weiss et al. 2003). The region of available oxygen surrounding the root is called the oxidized rhizosphere. The oxygen is either actively pumped or flows freely due to diffusion from the aerial portion of the plant to the roots through aerenchymatous tissue, which is tissue composed of large gas spaces called lacunae. The region of ferric and manganic oxide precipitation that occurs within the oxidized rhizosphere is clearly visible against the gleyed substrate (Christensen and Sand-Jensen 1998).

Vegetation Community

Ecological succession is the change in structure over time that can be observed in a vegetation community. As a system develops, the environmental conditions change either due to autogenic causes: vegetation and other organisms causing changes within the system (such as competition or the build up of organic matter); or allogenic causes: outside factors, such as changing climate patterns or build up of sediment brought in from outside the system. Generally, a combination of these changes determines the environment that is observed at a site at any given time. Secondary succession is the process of community development that occurs at a site after disturbance of the existing vegetation, but limited soil disturbance. Secondary succession is often very heavily influenced by the seed bank that is present, as well as other autogenic factors such as organic matter buildup (Smith and Smith 2001).

Primary succession is the sequence of vegetation that develops at a site that has not previously supported a vegetative community, such as newly exposed glacial moraines, volcanic soil, sand dunes, mine wastes, and created wetlands. In early successional stages, this process is predominantly controlled by allogenic factors. As the ecosystem matures autogenic factors start to play a greater roll and the system begins to resemble secondary successional communities (Noon 1996, Smith and Smith 2001, DeBerry and Perry 2004). Primary successional processes will be discussed in more detail later in this review.

WETLAND MITIGATION

Throughout history, human activity has lead to the destruction of wetland ecosystems. They have been drained and filled to create dry land for agriculture and development (Zedler 2004). Since the 1700's the wetland area in the United States has decreased by slightly more than 50% (Tiner 1984, Dahl 1990). In the 1970's as more research was being conducted in wetland ecosystems, the value of wetlands became clear. The Clean Water Act (CWA) (33 U.S.C. s/s 1251 et seq.) was designed to restore and protect the biological, chemical, and physical integrity of the nations waters, including wetlands. CWA section 404 regulates dredge and fill operations into protected waterbodies and along with the federal policy of "No net loss" of wetland structure and functions is the basis for the Army Corps of Engineers (ACoE) wetland permitting program (Federal Register CWA 1980). Under CWA section 404, a permit must be applied for when a proposed activity will result in negative impacts to a wetland ecosystem. The requirements for permit approval include minimization of all avoidable impacts and compensation for any unavoidable impacts. The compensation can be achieved by restoring a degraded wetland or creating a wetland in a location that was previously upland or open water. The restoration or creation of wetlands through the CWA section 404 permitting process is called compensatory mitigation, and requires the replacement or restoration of wetland functions equivalent to or greater than what was destroyed. This is in keeping with the commitment by President George H.W. Bush, in 1989, to a policy of "No net loss" of wetlands in the United States.

Monitoring

After a mitigation wetland has been completed, the vegetation development and hydrology are monitored as part of the permit requirements. The required monitoring period is often between five and ten years; this is much shorter than is needed to gauge the equivalence to natural systems. Many studies that have monitored created wetlands for longer than five years, have compared the results to reference wetlands, which are natural systems of the same wetland type that are generally adjacent to or nearby the created system. The comparisons are done to determine if created systems are structurally and functionally similar to equivalent natural systems. This is particularly important in identifying the degree to which they are adequately replacing the structure and function of the destroyed natural system (Stolt et al. 2000, Campbell et al. 2002, DeBerry and Perry 2004, Bruland and Richardson 2005).

When the required monitoring or other studies of mitigation site structure indicate that the site is not meeting the requirements of the compensatory mitigation permit, additional management usually takes place. Depending on the shortcomings of the created site, this can involve re-grading or filling to achieve the desired hydrology and water depth, or herbicide application to remove undesirable invasive plant species, such as *Typha* and *P. australis*. Most of the studies that have been conducted looking at the vegetation development of created sites have been limited to sites no older than 20 years (Noon 1996, DeBerry and Perry 2004, Atkinson et al. 2005, Spieles 2005). The lack of knowledge about how these sites develop over long periods of time makes it very hard to determine if the current management practices are facilitating the development of an ecosystem that will reach structural equivalence to natural ecosystems.

Many studies have outlined the differences in structure and function between created and reference wetlands (Stolt et al. 2000, Campbell et al. 2002, DeBerry and Perry 2004, Bruland and Richardson 2005). While most studies have compared soil properties and/or vegetation structure in natural and created systems it has been assumed by many researchers that if the structure is significantly different, the functionality of the wetland will also be different (Campbell et al. 2002). The policies that allow destruction of natural wetlands to be compensated for by construction of created systems have most likely lead to the loss of wetland function and value throughout the U.S. (Zedler 2004, Brooks et al. 2005).

Environmental Characteristics in Created Wetlands: Soils

Many processes contribute to the differences that have been observed in soil characteristics between natural and created wetlands. In created wetlands, the surface soil is removed during the creation process, resulting in a mineral subsoil at the surface that is largely devoid of organic matter (Atkinson et al. 1993). This creates a soil surface with very little microtopographic relief, resulting in lower habitat heterogeneity which can lead to reduced biodiversity (Stolt et al. 2000, Campbell et al. 2002, Brooks et al. 2005). In a study conducted in created wetlands in Virginia (Stolt et al. 2000) found that soil characteristics in created systems differed significantly from reference systems, and that created systems had a lower particle size range, higher sand percentage, and lower organic matter content. These soil characteristics result in a much lower water-holding capacity and higher permeability and porosity, all of which are important for maintaining correct hydrologic conditions in wetlands. Lack of palatable organic matter can also limit bacterial remineralization, therefore limiting available inorganic nutrients required for plant growth (McLatchey and Reddy 1998) as well as limit redox processes via a lack of metabolic electron sources.

Environmental Characteristics in Created Wetlands: Vegetation and Primary Succession

The vegetation community that develops in a created wetland is controlled by a variety of factors including creation method, water budget, proximity to propagule source, soil organic matter content, and nutrient availability. Vegetation development in created wetlands is often considered a form of primary succession. During the construction process the top layers of soil are removed in order to achieve the desired wetland hydrology; thus removing the existing seed bank and organic matter, leaving a mineral subsoil at the surface that has never supported vegetation. In some instances the higher organic content top soil is returned to the site, however there is still a large amount of site disturbance, and lack of a wetland seed bank (Atkinson et al. 1993, Cronk and Fennessey 2001). Created wetland construction techniques often involve seeding and plantings; this practice is meant to facilitate the development of the desired vegetation community. Even in planted sites, there are many plants that come into the system as colonizers (Reinartz and Warne 1993). The species that colonize a site are determined by the surrounding natural ecosystems and the introduction pathways into the site. Isolated wetlands that have no surface water connections to other water bodies, are often dependant on colonizers with wind dispersed seeds (Gleason 1952, Reinartz and Warne 1993). Riverine systems receive a lot of throughflow, and therefore many water-dispersed colonizers are able to establish in these sites. The initial competitive dynamics associated with propagule dispersal can have important and long lasting ecological consequences on long-term species dynamics, even when seeding/planting has occurred (Noon 1996, DeBerry and Perry 2004).

Initial colonization of the bare mineral soil of a created wetland is dependant on the type of propagules that are transported to the site, as well as the occurrence of required resources for establishment of the seeds. Therefore, adjacent ecosystems can be an important control on the initial community composition in created systems (Noon 1996). The created wetland primary succession model developed by Noon (1996) states that there are two phases of early primary succession. The first phase includes the changes that occur in the first three years after wetland creation. In this phase, called the

Arrival and Establishment Phase, the community development of the system is primarily controlled by allogenic factors such as chance of recruitment. The initial vegetation is generally composed of highly competitive, quickly reproducing annuals, and perennials that are able to utilize annual-like strategies (DeBerry and Perry 2004). These types of plants are able to take advantage of the high availability of low organic matter soil (Noon 1996). This phase is often dominated by graminoid, or grass-like, species that are able to reproduce both clonally and through seed dispersal, therefore increasing their ability to quickly colonize available soil. Noon (1996) also showed that during the Arrival and Establishment Phase, newly created wetlands had higher species richness and diversity compared to older created sites. Newly created sites also had a percent aerial cover of only 50-60%, lower than the greater than 90% that was observed at more developed sites. This is most likely due to the initial colonization by a large number of species, that are then whittled down to a lower number as the highly competitive varieties outcompete the less competitive species and are able to expand into the remaining open soil.

In his study, Noon observed a shift from graminoid species dominance of the herbaceous community during the first 4 years to dominance by forbs in sites that were eight to eleven years old. It is this later forb dominated community that Noon (1996) termed the Autogenic Dominance Phase. He postulated that development during this phase is dominated by vegetative factors such as organic matter build up from the senescence of above and belowground primary production and seed bank creation, as well as interactions among species, including competition and facilitation. While it is thought that during this phase autogenic factors exert the most control over community development, allogenic factors can still play an important role in determining the course of succession.

The life histories of the species that are able to colonize during the initial Arrival and Establishment Phase will largely control the community development in later successional phases. A study by DeBerry and Perry (2004) investigated the vegetation characteristics of a created wetland and compared it to Noon's model (1996). They did not find the same trends predicted by Noon; the vegetation communities in the newly created sites they studied were mainly comprised of perennials and facultative annuals. This may indicate that wetland perennials may exhibit "annual-like" strategies in order to rapidly exploit available soil in newly created wetlands (DeBerry and Perry 2004).

Invasive Wetland Plants

Invasive species are populations that establish, proliferate, and persist in a new or expanded range to the detriment of the endemic community (Galatowitsch et al. 1999, Zedler and Kercher 2004). Invasive species can include non-native species; hybrids, either between two native species or between a native and a non-native species; as well as native species (Mack et al. 2000). Invasiveness in both native and non-native wetland plants is often facilitated by anthropogenic changes in environmental conditions such as salinity, hydrologic flow, and nutrient availability (Galatowitsch et al. 1999, Ellstrand and Schierenbeck 2006, Woo and Zedler 2002). Phosphorus enrichment from agricultural runoff in the Florida Everglades has lead to the expansion of *Typha domingensis* Pers. (southern cattail) dominated communities (Urban et al. 1993, Childers et al. 2003, Zedler and Kercher 2004). Hybridization can also facilitate invasion, as hybrids are often able to exploit environments in which neither of the parent species are able to thrive (Zedler and Kercher 2004). This has been observed in many species, including *Typha* x *glauca* Godr. (cross between *Typha angustifolia* L. and *Typha latifolia* L.) (Ellstrand and Schierenbeck 2006), *Spartina angelica* C. E. Hubbard (cross between *Spartina alterniflora* Loisel. and *Spartina maritima* M. A. Curtis) (Galatowitsch et al. 1999), and the lineage created by the cross between *Lythrum salicaria* L. and *Lythrum alatum* Pursh (Ellstrand and Schierenbeck 2006).

Invasive plant species have the potential to alter large-scale ecological processes in wetlands (Galatowitsch et al. 1999). Monospecific stands of invasive plants not only decrease species richness, but can also lessen the ability of the system to filter out certain types of pollutants and nutrients (Ehrenfeld and Scott 2001). Other ecosystem alterations include changes in geomorphological processes such as erosion and sedimentation rates, surface elevations, biogeochemical processes including nutrient mineralization and immobilization rates, and hydrological processes such as water table depth (Ehrenfeld and Scott 2001, Engelhardt and Ritchie 2001, Ehrenfeld 2003). Other studies have also shown that invasive species can alter fire regimes by changing fuel properties, and sometimes altering local microclimate and preventing regional successional patterns (D'Antonio and Vitousek 1992, Brooks et al. 2004). The impacts of invasive plant species on wetlands are often specific to the environmental conditions unique to each wetland ecosystem.

Typhaceae in North America

The family Typhaceae includes the species in the genus *Typha,* commonly referred to as cattails. *Typha* are common herbaceous wetland plants that reproduce clonally as well as through propagule distribution. They are extremely prolific and tend to form dense monospecific stands, especially in wetlands that have experienced anthropogenic disturbances, such as changes in hydrology, and nutrient input (Miao and Sklar 1998, Newman et al. 1996). *Typha* have been observed forming dense monocultures in disturbed natural wetlands as well as created and restored wetlands (Green and Galatowitsch 2001).

Typha Life History

Typha are monoecious, perennial, rhizomatous herbs that reproduce both clonally and through propagule dispersal. They are all obligate wetland indicator species (USFWS, 2006). The four species found in North America, *Typha angustifolia* L., *Typha latifolia* L., *Typha* x *glauca* Godr., and *Typha domingensis* Pers. are all characterized by narrow, blade-like, leaves that are sheathed at the base. The leaves are often between 1-3 m in length, with one terminal cylindrical inflorescence per shoot on which both staminate (above) and pistillate (below) flowers are found (Gleason 1952). Inflorescence spikes are varying widths, but are generally dark brown to green, with deciduous staminate flowers. Seeds are wind dispersed and germinate on saturated soil or under shallow water.

T. angustifolia (narrow leaved cattail) has leaves that grow to a height of 1-1.5 m and are 3-8 mm wide. The leaves are often much taller than the inflorescence, and are strongly convex on the back (Gleason 1952, Beal 1977). Like all *Typha* species, it has a spike-like terminal inflorescence. However, it can be distinguished by a space of 1-8 cm between the staminate and pistillate flowers. The pistillate portion of the spike is generally 10-20 cm long and 8-15 mm thick at maturity and is dark brown to reddish brown (Gleason 1952).

T. domingensis (southern cattail) is slightly taller than *T. angustifolia* at 2-3 m, with more numerous leaves (Gleason 1952). The leaves are generally 6-15 mm wide and are slightly convex on the back. The inflorescence is as tall as or slightly taller than the leaves. The staminate and pistillate spikes are generally separated as in *T. angustifolia*, however the pistillate flowers are lighter brown in color than *T. angustifolia* (Beal 1977).

T. latifolia (common cattail) is characterized as having taller (2-3 m) and wider (5-24 mm) leaves than the other species. Leaves are flat and generally exceed the inflorescence in height. The staminate and pistillate spikes are contiguous. The pistillate spike is 2.5 cm thick at maturity, and ranges in height from 5 to 20 cm (Beal, 1997).

T. x *glauca* is the hybrid of *T. angustifolia* and *T. latifolia*. It generally has intermediate morphology between both parent species. The leaves are 1-3.5 m tall, 7-10 mm wide, and moderately convex on the back (Beal 1977). The staminate and pistillate flowers are usually separate, with the pistillate spike up to 50 cm long and 1.6-2 cm in diameter (Beal 1977). Many studies have attempted to determine if *T.* x *glauca* can be readily distinguished from *T. angustifolia* and *T. latifolia* based on morphological characteristics (McManus et al. 2002, Kuehn and White 1999, Sharitz et al. 1980). However, it appears that the overlap of morphologies is such that a definitive identification cannot be made without genetic analysis (Kuehn and White 1999).

T. latifolia is the most common cattail in North America, and is found throughout the United States (Beal 1977). It is confined to shallow water, generally less than 0.5 m (Grace and Wetzel 1998), and is only found in freshwater. It is currently under debate whether or not *T. angustifolia* is native to North America or was introduced by European settlers, as has been suggested by Stuckey and Salamon (1987). Until the early 19th century *T. angustifolia* was found only in freshwater and brackish marshes of the Atlantic coastal plain (Finkelstein 2003). Regardless of its origin it began to expand westward along with the increased development of roads and railways that occurred in the 1800's (Galatowitsch et al. 1999, Finkelstein 2003). It now extends across much of the United States. *T. angustifolia* is generally found in deeper water (0.5 to 1 m) than *T. latifolia* and is able to grow in both fresh and brackish water. The differentiation due to water depth between *T. angustifolia* and *T. latifolia* has been shown to persist for long periods of time, because *T. angustifolia* is unable to compete with *T. latifolia* in shallow water and is therefore relegated to deeper water (Grace and Wetzel 1998, Cronk and Fennessey 2001). *T.* x *glauca* is found in many areas where both parent species are present. It is often much less abundant than either parent species, but has been shown to out compete them in some nutrient enriched systems (Ellstrand and Schierenbeck 2006). *T. domingensis* is found in the southern United States, and is common in the Everglades region of Florida. It was historically found in small patches throughout the Everglades system, but in recent years has spread and now covers large portions of the Everglades (Stewart et al. 1997).

Typha spp. as Invasives

Many *Typha* species have been shown to be invasive in disturbed environments. They are quick colonizers of sites that have undergone nutrient enrichment. This has been documented for *T. latifolia, T.* x *glauca,* and *T. domingensis* (Newman et al. 1996, Woo and Zedler 2002, Childers et al. 2003). The spread of *T. domingensis,* a competitive, high-nutrient status species, is thought to be related to increased nutrient enrichment due to agricultural practices within the Everglades watershed (Craft et al. 1995, Stewart et al. 1997, Richardson et al. 1999). The Everglades is a historically oligotrophic ecosystem characterized by *Cladium jamaicense* (Crantz) a stress tolerant low-nutrient status species (Richardson et al. 1999); with *T. domingensis* found in small restricted patches (Childers et al. 2003). In a study by Miao and Sklar (1998) the life history characteristics and resource allocation in both *C. jamaicense* and *T domingensis* were analyzed. They found that *T. domingensis* is adapted to high resource availability, has high individual and population growth rates, short lifecycles, high propagule dispersal over large areas, and a rapid plastic response to changes in resource availability. These characteristics allow it to quickly take advantage of high nutrient concentrations, allowing it to quickly establish itself during periodic pulses of high nutrient levels. This is consistent with a study showing that *T. domingensis* density increased more rapidly during typically wet years (Urban et al. 1993). It has been postulated that the addition of nutrients alone may not be the main factor in *T. domingensis* expansion in the Everglades, the alteration of the hydroperiod through water conservation projects may also be a major factor in allowing *T. domingensis* to expand its range (Stewart et al. 1997).

Other *Typha* species have also been documented as invasives in nutrient enriched systems. *T.* x *glauca* has formed monotypic stands in natural wetlands previously dominated by *Carex* (Woo and Zedler 2002) and invaded restored prairie pothole wetlands influenced by agricultural runoff (Green and Galatowitsch 2001). *T. latifolia* has also been documented as an invasive in created, restored, and nutrient enriched systems (Mitsch and Gosselink 2001). It has been shown in mesocosm experiments to outcompete *Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla , under conditions of both nitrogen and phosphorus enrichment (Svengsouk and Mitsch 2001).

Hybridization can also facilitate invasion, as hybrids are often able to exploit environments in which neither of the parent species are able to thrive (Ellsatrand and Schierenbeck 2000). *T.* x *glauca,* the hybrid species produced from *T. latifolia* and *T. angustifolia,* has been reported to be equal or dominant to both parent species at some sites (Smith 1967). It seems to be able to exploit ecosystem disturbances in much the same way as the parent species. There have not to my knowledge been any studies illustrating *T.* x *glauca* directly outcompeting either parent species, however its ability to establish itself in habitats already dominated by *T. latifolia* and *T. angustifolia* indicate that it is able to compete with both parent species to some extent.

Chapter 2: Methods

Objectives

The overall objective of this study was to better understand how environmental factors, such as nutrient availability, elevation, and soil organic matter, may influence the dominance of *Typha* in created palustrine forested wetlands. As well as to determine if there is evidence that *Typha* is an invasive species in these systems. In order to fulfill these objectives I compared the vegetation community, soil characteristics, and nutrient availability in two young, less than five years old, to two 14-year-old created forested wetlands. Two stands in each wetland, one dominated by *Typha* and one dominated by other wetland species, were sampled in each created wetland. The vegetation community of each stand was measured throughout the sampling period and analyzed to determine if community composition showed significant differences in species dominance between young and mature created wetlands. The soil nutrient availability was also monitored to determine if there was a difference in *Typha* and non-*Typha* assemblages as well as between sites of different ages

Hypotheses

H_O1: Plant species composition, diversity, and peak season standing crop (total and per species) in *Typha* dominated stands and non-*Typha* dominated stands will not vary between older and newer sites.

H_O2: Soil organic matter content and porewater and soil inorganic nutrient availability (N and P) will not vary between older and newer sites.

H_O3: Soil organic matter content, and porewater and soil inorganic nutrient availability (N and P) will not vary between stands dominated by *Typha* and stands not dominated by *Typha* within a single site.

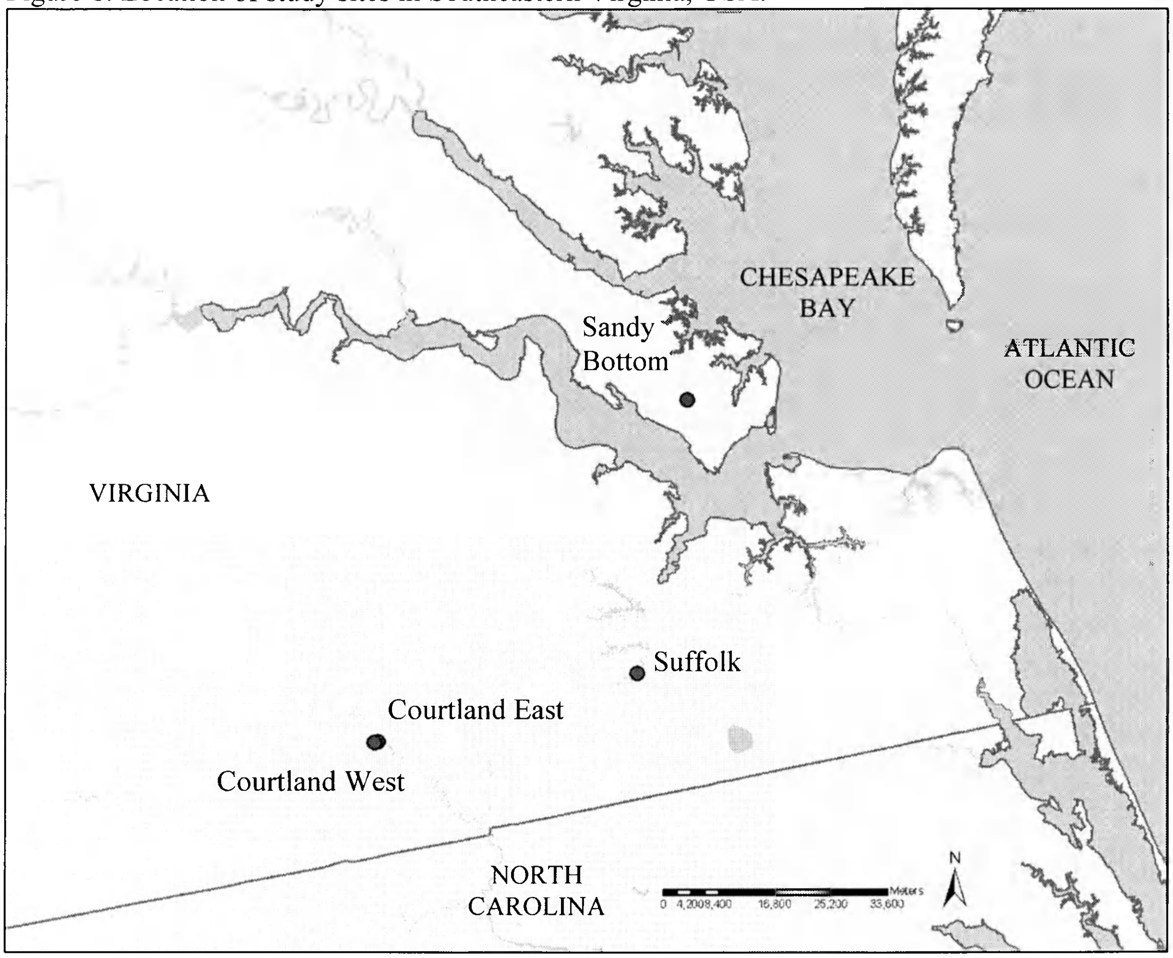
H_O4: *Typha* leaf nutrient concentrations (N and P) and C:N:P ratios will not vary between older and newer sites.

H_O5: Phosphorus uptake rates of *Typha* will not vary at different N:P ratios.

Site Descriptions

Four sites, all created palustrine forested wetlands (PFO) constructed by the Virginia Department of Transportation (VDOT) and located in the Coastal Plain physiographic province of Virginia, were used in this study (Figure 1). Three sites, Suffolk Bypass (SF), created in 2003, Courtland Bypass East (CE), and Courtland Bypass West (CW), both created in 1993, were sampled during the summer of 2006 (June to September). These sites as well as a fourth mitigation site located in Sandy Bottom Nature Park (SB) created in 2005, were sampled during the summer of 2007 (April to September; Figure 1). These sites were selected since each had vegetation guilds that were 1) dominated by *Typha* and 2) were dominated by wetland species other than *Typha*. The sites also represent a group of older, more mature sites (CE and CW) and more recently constructed sites (SF and SB) that allowed a comparison of plant communities and nutrient dynamics between sites of different ages and successional stages.

Figure 1: Location of study sites in Southeastern Virginia, USA.



Suffolk Bypass Mitigation Site

Suffolk Bypass site (SF) is located near Suffolk, VA, adjacent to Lake Kilby and the Kilby Shores subdivision. It is 5.19 ha in size (Figure 2) and is located in the southeastern Coastal Plain physiographic province. It is characterized by nearly level topography and mineral soils of maritime origin. The wetland was constructed in 2002 as compensatory mitigation for wetlands affected during construction of southwest Suffolk US HWY- 460 Bypass. The site was previously used for sand mining and as a borrow pit and is surrounded by slopes up to 10 m in relief. The surrounding landscape includes a moderate-density residential community, as well as some agriculture and forested land. SF functions primarily as a slope wetland with a gentle gradient; capture of surface runoff and ground water seepage are the primary sources of water.

During construction, the site was filled with imported material, including topsoil that had been stripped and stockpiled. An organic amendment was added to the site that was composed if partially composted yard waste. This amendment resulted in initial topsoil OM ranging between 2 and 5% (pers. comm. W. L. Daniels). Wetland hydrology at SF was approved in August 2003 and the site was subsequently planted in the fall of 2003. SF was designed to support 85% forested, 9% scrub-shrub, and 6% emergent wetlands. Woody species planted at the site include *Taxodium distichum* (bald cypress), *Nyssa aquatica* (water tupelo), *Pinus seratina* (pond pine), and *Quercus lyrata*, (overcup oak) (Daniels et al. 2005). In June of 2007, a large portion of the vegetation at the site was cut by Virginia Department of Transportation as part of their *Typha* control measures. The majority of the first *Typha* stand was cut and so sampling was continued in an adjacent area that had not been cut (Figure 2).

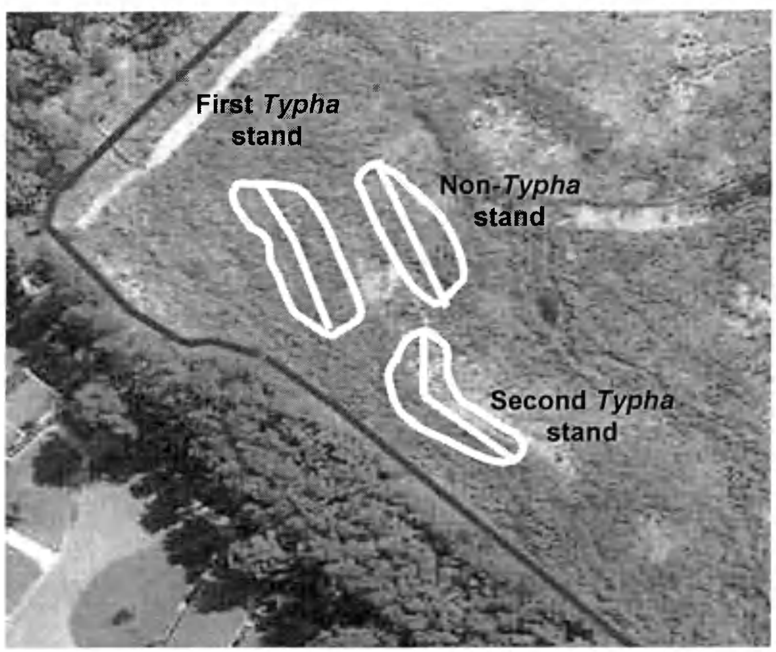
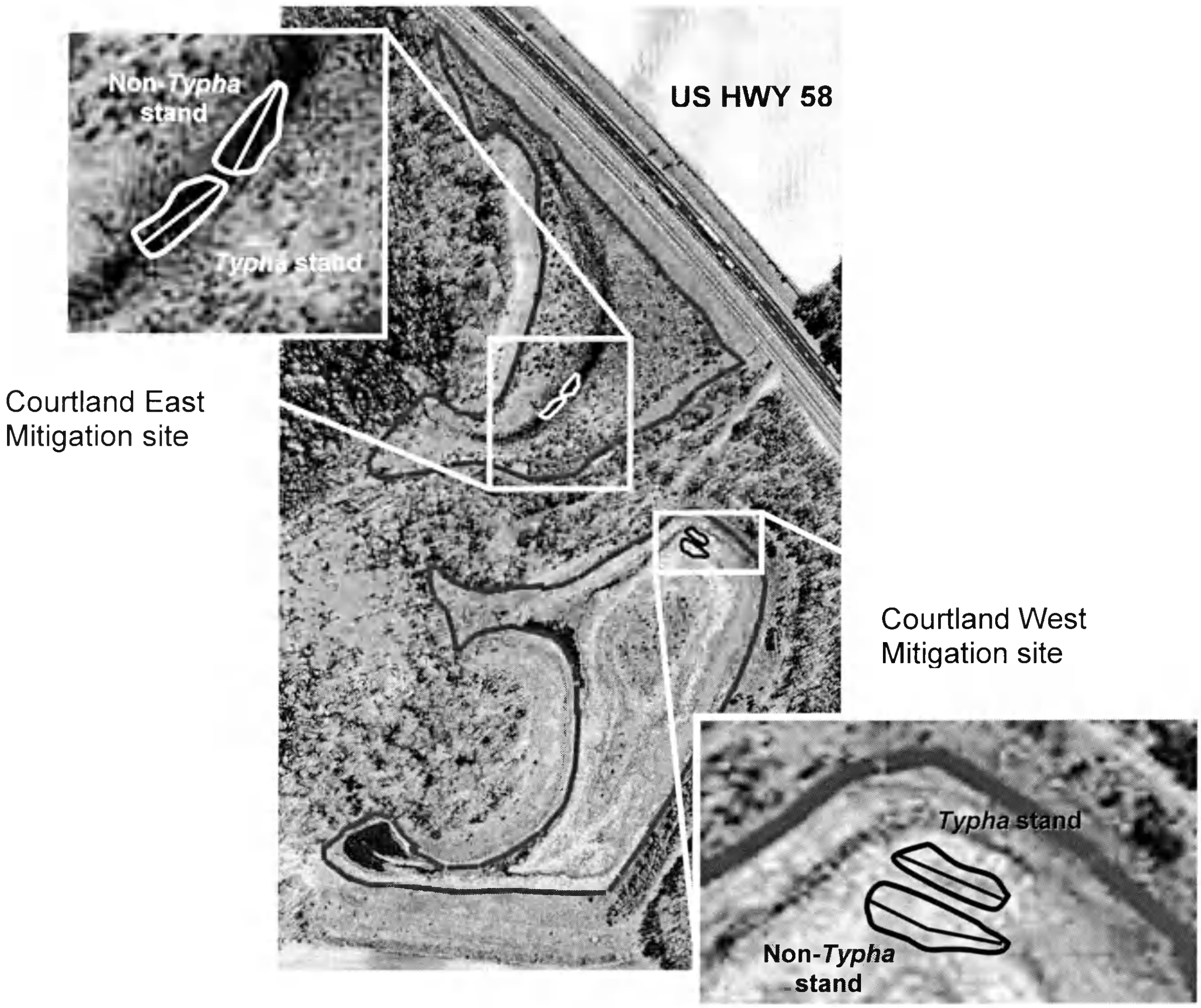


Figure 2: Aerial photographs of Suffolk Bypass mitigation site, with close-up of study area, *Typha* and non-*Typha* stands with baselines delineated.

Courtland East and West

The Courtland mitigation sites are two non-contiguous sites located off US Route 58 near Courtland, VA (Figure 3), both were completed in 1993. Courtland East (CE) is 1.91 ha and Courtland West (CW) 3.18 ha in size. The sites are located in the Coastal Plain and have gentle topography and a prevalence of sandy soils along the perimeter, underlain by silty clay loam substrates with high organic accumulations. They are adjacent to the Nottoway River floodplain, and the surrounding landscape is predominantly agricultural with a significant amount of forested area. The hydrology of both sites is derived from groundwater discharge and capture of surface water. Both sites were planted with woody species, including *Taxodium distichum* (bald cypress), *Nyssa aquatica* (water tupelo), *Quercus nigra* (water oak), *Fraxinius pennsylvanica* (green ash), and *Quercus palustris* (pin oak); shrubby species, including *Alnus serrulata* (common alder), *Gelsemium sempervirens* (Carolina jessamine), *Parthenocissus quinquefolia* (Virginia creeper), *Morella cerifera* (wax myrtle), *Viburnum nudum* (southern wild raisin), *Vaccinium corymbosum* (high bush blueberry), and *Magnolia virginiana* (sweetbay magnolia); as well as herbaceous species such as, *Iris versicolor* (blue water iris), *Peltandra virginica* (arrow arum), *Pontedaria cordata* (pickerel weed), *Saururus cernuus* (lizard's tail), *Acorus calamus* (sweet flag), *Sagittaria latifolia* (duck potato), and *Panicum virgatum* (switch grass).

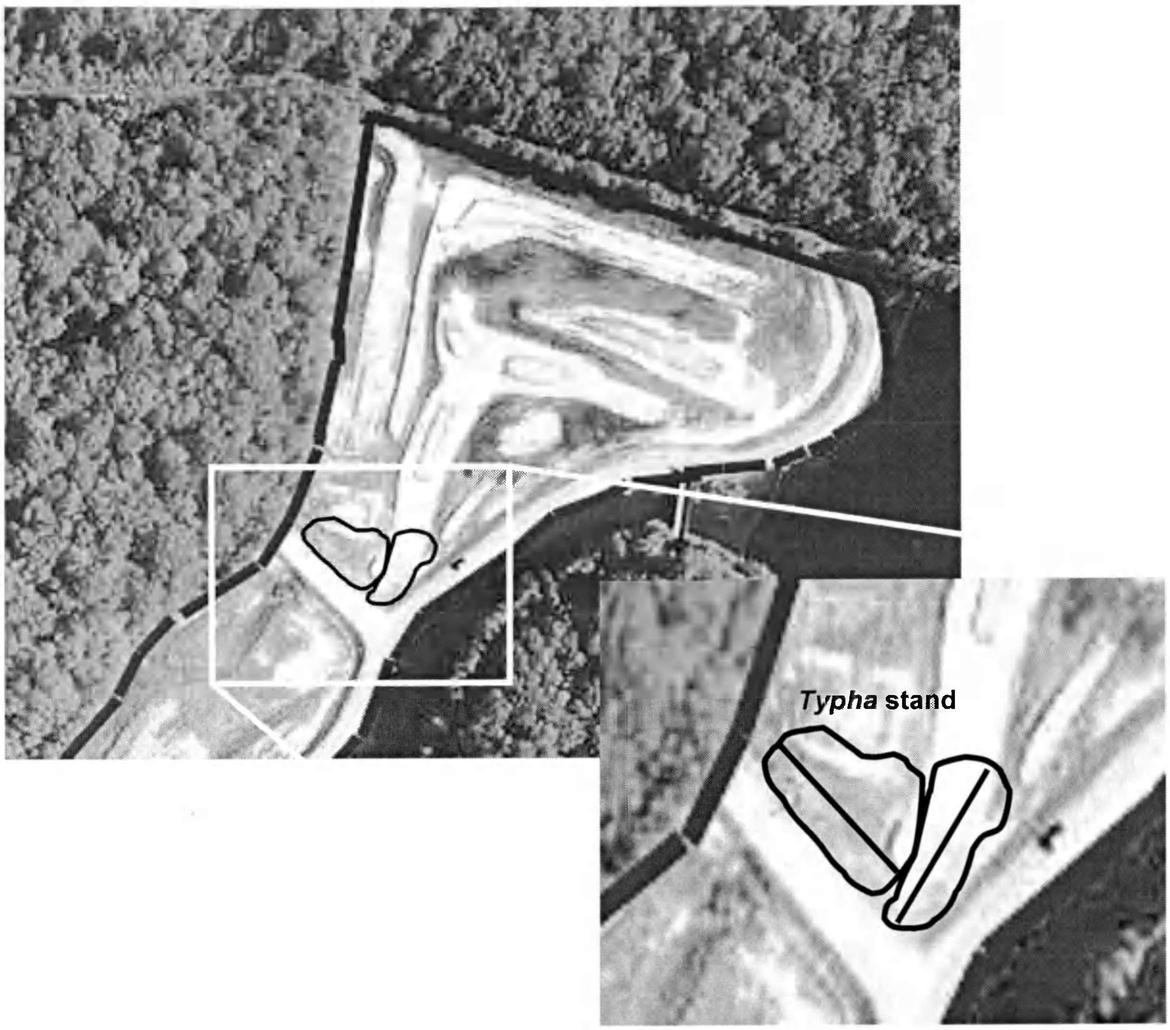
Figure 3: Aerial photograph of Courtland East and West mitigation sites, with close up of study areas; *Typha* and non-*Typha* stands with baselines delineated.



Sandy Bottom Nature Park

The Sandy Bottom mitigation site is 17.48 ha in size (Figure 4) and is located between I-64 and Hampton Roads Center Parkway, in Hampton, VA. The site was originally used for sand mining and as a borrow pit, therefore, filling and grading were required to achieve the desired elevation. During construction, the site was filled with imported subsoil that was compacted and contained higher clay content than the soil in the surrounding natural wetlands. This led to perching of water in the surface soil layers. Compost amended topsoil was then added and disked in to depth of 20 cm (Daniels et al. 2005). Planting at the site occurred in the fall of 2004; forested species included *Quercus lyrata* (overcup oak), *Quercus phellos* (willow oak), *Taxodium distichum* (bald cypress), and *Nyssa aquatica* (water tupelo). Emergent and scrub-shrub species included *Alnus serrulata* (common alder), *Viburnum dentatum* (southern arrowwood), *Photinia floribunda* (purple chokeberry), *Saururus cernus* (lizard's tail), *Lobella cardinalis* (cardinal flower), and *Iris virginica* (blue water iris).

Figure 4: Aerial photograph of Sandy Bottom mitigation site, with close up of study areas; *Typha* and non-*Typha* stands with baselines delineated.



Field Sampling and Laboratory Analysis

Sampling Design

At each study site, two adjacent areas were identified with similar water depth: one dominated by *Typha* and one dominated by other wetland species. Dominance by *Typha* was determined by >20% *Typha* aerial cover. The determination of *Typha* only to the genus was necessitated by the inability to reliably identify to the species level in the field (McManus et al. 2002, Kuehn and White 1999, Sharitz et al. 1980). Within both the *Typha* dominated (T) and the non-*Typha* (NT) stands, a baseline transect at least 30 m was designated and marked with flags. All sampling was done within the stands at random distances along and from the baseline. The locations of the stands and baselines can be seen in the aerial photographs of each site (Figures 2, 3, and 4)

Monthly sampling

Field sampling occurred monthly at each site, from June to October 2006 and April to September 2007. Three 1 m^2 quadrats were sampled within the NT and T stands on each site.

The following parameters were measured in standing water in each quadrat (NT and T):

1) Water depth: measured as the mean of three locations within each 1 m^2 quadrat.

2) Vegetation percent cover: estimated visually as a value of 1% to 100% or trace (<1%). Values are based on a modified Braun-Blanquet cover scale where: <1% = trace, (1-5%) = 2.5%, (6-10%) = 7.5%, (11-25%) = 17.5%, (26-50) =

37.5%, (51-75%) = 62.5%, (76-98%) = 87.5%, and (98 to 100%) = 99% (Daubenmire 1959).

3) Two soil samples were taken to a depth of 10 cm with 2 cm diameter corer, bagged, returned to lab, refrigerated, and freeze dried or dried in a Fisher Scientific Isotemp drying oven at 80° C. Samples were then ground, using mortar and pestle, homogenized and put through a 2 mm sieve.

In T quadrats only, the above parameters were sampled as well as the following:

4) *Typha* ramet density, including total live shoots, flowering shoots, and standing dead shoots.

5) *Typha* leaf tissue samples: 3 samples of the 4th leaf from the intercalary meristem were collected in each quadrat. Samples were dried in a Fisher Scientific Isotemp drying oven at 60° C until they achieved constant mass. They were then homogenized by milling and passing through a No. 40 mesh screen using a Thomas Scientific Wiley Mill.

<u>Bi-monthly porewater sampling</u>

Diffusion samplers, also called peepers, were used to measure porewater nutrient concentrations in both T and NT stands at each site. The diffusion samplers have four rows of three wells. Rows are at 5 cm intervals from the soil surface to a depth of 20 cm (Figure 5). The wells were filled with deionized water and a 0.2 μm membrane filter was placed over the opening to the wells and held in place by a top plate attached by screws (Figure 6) (Hesslein 1976, Winger et al. 1998).

Porewater samples were collected in April, June, and August of 2007. Two diffusion samplers were set in the soil at random locations in both T and NT stands at all study sites. They were allowed to equilibrate for a minimum of three weeks after deployment, then removed, and the water samples collected. Water from the first two wells in each row was filtered through a 0.45 μm filter. Filtered samples were preserved with 0.5 ml 1N HCl, returned to the lab, and stored in Fisher Isotemp refrigerator, for no more than 3 weeks, until phosphate and ammonium analysis was conducted. Porewater pH was measured in the field from the water in the third well using a Beckman Instruments model # 123133 pH meter.

Figure 5: Porewater sampling depths.

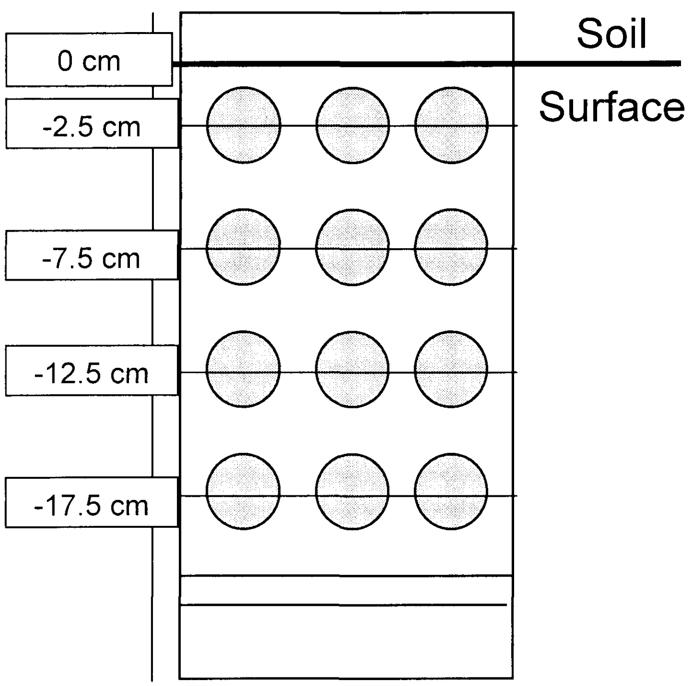
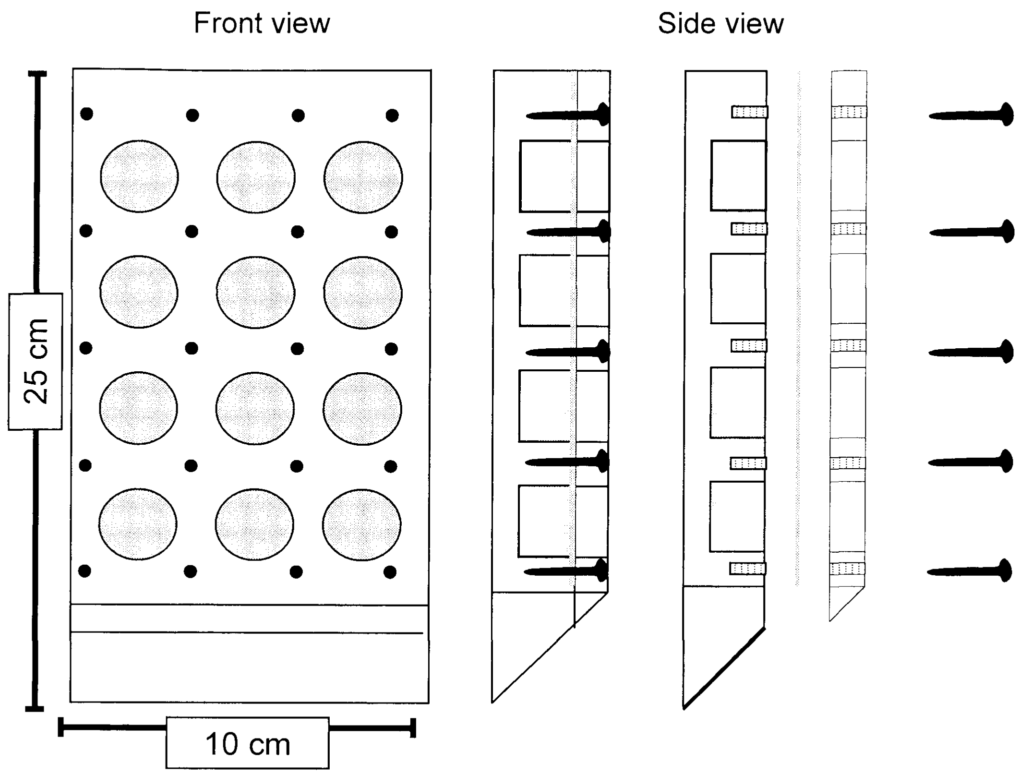


Figure 6: Schematic of diffusion sampler used for porewater sampling.



Lab Analyses

Organic matter content was determined for plant and soil samples. Samples were dried in a Fisher Scientific Isotemp Oven. Plant samples were milled using a Thomas Scientific Wiley Mill and homogenized. Soil samples were ground with a mortar and pestle and passed through 2mm sieve. A portion of each sample was weighed, combusted in a Fisher Scientific Isotemp Muffle Furnace, and weighed again to determine ash free dry mass (AFDM).

A portion of the homogenized soil sample was analyzed for acid extractable phosphorus (AEP) by conducting an 18 hour 1 N HCL extraction at room temperature (Solorzano and Sharp 1980, Chambers and Fourqurean 1991, Chambers et al. 1995). Another sub-sample, soil total phosphorus (TP), was combusted and extracted in 1 N HCl following the same procedure as AEP. After 1 N HCL extraction the phosphate concentrations in both the TP and AEP subsamples were quantified using ascorbic acid colorimetric phosphate determination (Parsons et al. 1984). The difference between TP and AEP measurements was determined to be the organic phosphorus (OrgP) soil fraction.

Porewater samples were analyzed for dissolved inorganic phosphate (DIP) using the ascorbic acid colorimetric phosphate determination (Parsons et al. 1984). The total dissolved phosphorus (TDP) concentration in porewater was estimated by evaporating 10 ml of filtered samples and combusting the evaporite in a Fisher Scientific Isotemp Muffle Furnace at 400^{o} C for three hours. The combusted evaporite was then resuspended in 5 ml of 0.2 N HCl, capped, and extracted for 1 hour at 80^{o} C. The samples were then diluted and phosphate concentrations determined by ascorbic acid colorimetric determination (Parsons et al. 1984). Porewater ammonium was quantified using sodium citrate colorimetric determination.

Typha leaf tissue was weighed, combusted, and analyzed for TP by extracting the combusted sample in 0.2 N for 1 hr at 80^{o} C. The TP concentration was then measured using the ascorbic acid colorimetric phosphate determination method (Parsons et al. 1984). Total nitrogen and total carbon in soil and plant tissue samples were measured using the Perkin-Elmer CHN 2400 Series II Elemental Analyzer.

Uptake Rates

Rhizomes, each containing at least one terminal or basal node, were collected in early December 2006 and were planted in a sand mixture in the College of William and

Mary greenhouse. The rhizomes were clipped to 4 cm in length, with all fibrous root and dead stem material clipped to less than 1 cm. Each rhizome was dipped in 90% sulfur fungicide prior to planting. Plantings were allowed to develop in the greenhouse for two months.

Twenty-four two-month old plantings were then used to measure nutrient uptake kinetics under a range of nutrient limitations. Eight plantings were placed in solutions containing three ratios of N:P (Table 3) in the form of ammonium (NH_4^+) and phosphate (PO_4^{3-}). Ammonium was used since it is the primary form of bioavailable N in submerged wetland soils (Mitsch and Gosselink 2000). The PO_4^{3-} concentration was 50 μM in all treatments and was based on the mean PO_4^{3-} concentration in preliminary porewater samples measured at the Suffolk site in October 2006.

Table 3: Phosphorus uptake experiment nutrient concentration

Treatment	NH_4^+ Concentration	PO_4^{3-} Concentration	N:P ratio
1	50 μM	50 μM	1:1
2	150 μM	50 μM	3:1
3	0 μM	50 μM	0:1

Four runs were conducted with six plants (two replicates per treatment during each run), over four days in controlled lab conditions with ambient light and at room temperature. Plants were placed in 1000 ml beakers with the nutrient solution and a magnetic stirrer. The solution was stirred continuously and 10 ml aliquots were removed at intervals of 0, 20, 40, 60, 120, and 180 minutes. The 10 ml samples were analyzed using colorimetric methods for NH_4^+ and PO_4^{3-}. (Claassen and Barber 1974, Bradley and Morris 1991, Dyhr-Jensen and Brix 1996, Brix et al. 2002).

DATA ANALYSIS

Herbaceous Vegetation

Percent cover data was collected once a month using a modified Braun-Blanquet cover scale (Daubenmire 1959, DeBerry and Perry 2004), with plant taxonomy and nomenclature following Beal (1977), and Natural Resources Conservation Service Plants Database (USDA, NRCS 2006). The estimates of cover and frequency were converted to relative measures and summed to calculate importance values (IV) for each species in both NT and T stands at each site (Atkinson et al. 1993). The IV was averaged across all quadrats in each stand and over the growing season to obtain an average IV for both the T and NT stands at each study site. The dominant species in each stand were selected by ranking in order of decreasing IV with dominants comprising the first 50% of the total IV as well as any additional species that make up greater than 20% of each sample; 50:20 rule (US Corps of Engineers 1987).

Species richness (SR) was determined as the total number of species for each stand. Evenness (J') and the Shannon Diversity Index (H') (Zar 1999) were calculated using the relative IV data for each stand and the following equations, where k is the number of species, p_i is the proportion of total IV for species i:

$$H' = -\sum_{i=1}^{k} p_i \log p_i$$

$$J' = \frac{H'}{H'_{\max}} \quad \text{where } H'_{\max} = \log k$$

The Ellenberg Community Coefficient Similarity Index (SI_E) (Mueller-Dombois and Ellenberg 1974) was calculated and used to compare the similarity of the plant communities between the stands within sites as well as to compare the stands in different sites, using the following equation; where M_a is the total IV for the species found only in site a, M_b is the total IV for species found only in site b, and M_c is the total IV for species found in both sites a and b:

$$SI_E = \frac{(M_c / 2)}{(M_a + M_b + M_c / 2)}$$

Weighted Averages were calculated for each species as the product of the sum of per stand IV for each month and the indicator index of that species (Region 1, Reed 1988). Indicator values ranged from 1 (OBL) to 5 (UPL), with intermediate indicators assigned in between (FACW+ =1.67, FACW = 2, FACW- = 2.33, FAC+ = 2.67, FAC = 3, FAC- = 3.33, FACU+ = 3.67, FACU= 4, FACU- = 4.33). The monthly values were then averaged over the growing season, in order to determine the similarity of the USFWS wetland indicator status (Reed Jr 1988, Atkinson et al. 1993) of the plants within each stand. This calculation is summarized in the following equation, where n is the number of species, $x_1, x_2....x_n$ are the relative IV values for each species in the stand, and $w_1, w_2, \ldots, w_n$ are the indicator values of each species:

$$WA = \frac{(x_1 w_1 + x_2 w_2 + \ldots + x_n w_n)}{\sum_{i=1}^{n} x_i}$$

The total IV of annuals, perennials, and facultative annuals was calculated to compare to proposed models of primary succession (DeBerry and Perry 2004, Noon 1996, van der Valk 1981). The mean monthly water depth was calculated by averaging the depths in the three monthly quadrats. The hydrograph of the T and NT stands were compared for each site using Repeated Measures Analysis of Variance (SPSS v. 16). Values for soil organic matter, total carbon, total nitrogen, acid extractable phosphorus, total phosphorus, and organic phosphorus were analyzed for differences between T and NT stands within each site, and between sites (with T and NT grouped) using Repeated Measures Analysis of Variance (SPSS v. 16). The monthly porewater values, averaged over the 20 cm sampling depth, were also analyzed for differences between T and NT stands within each site, and between sites using Repeated Measures Analysis of Variance (SPSS v. 16)

Principal components analysis (PCA) (Minitab 15) was used to compare the strength of the loadings on all sites. The bi-monthly means (April, June, and August) of soil and porewater parameters in all sites were used because porewater was only measured every other month. The soil and porewater parameters were analyzed for all T and NT stands in all sites. *Typha* ramet density, leaf N:P, and soil and porewater nutrient availabilities were analyzed for T stands at all sites.

CHAPTER 3: VEGETATION COMMUNITY COMPARISONS

RESULTS

Water depth and wetland indicator species

Repeated measures analysis of variance (ANOVA) revealed that there was a significant difference in water depth for *Typha* (T) versus non-*Typha* (NT) stands for all sites during 2007 sampling season ($p < 0.05$) (Figures 7a-d). All of the sites except CW were dry (albeit saturated to the surface) in both T and NT stands during at least one month during the growing season. SB was dry June, August, and September sampling, and also experienced the widest range of water depths (0 to 33 cm) (Figure 7a). This may be related to epiaquic soil layers, or clay pans, which cause perching of surface water and prevent groundwater from moving up through the soil profile. SF had the shallowest maximum water depth of any site, ranging from 0 to 7 cm; all other sites had maximum depths of greater than 20 cm (Table 4). These results indicate that dense *Typha* stands seem to occur in deeper water. However, there is no identifiable maximum water depth at which NT stands occur. The range of all T and NT water depths at all sites overlap with one another (Table 4), indicating that water depth may be one of the factors in *Typha* density, but it is not the main control.

Figure 7a. Mean (± 1 SE) monthly water depth at Sandy Bottom, summer 2007 growing season (April to September).

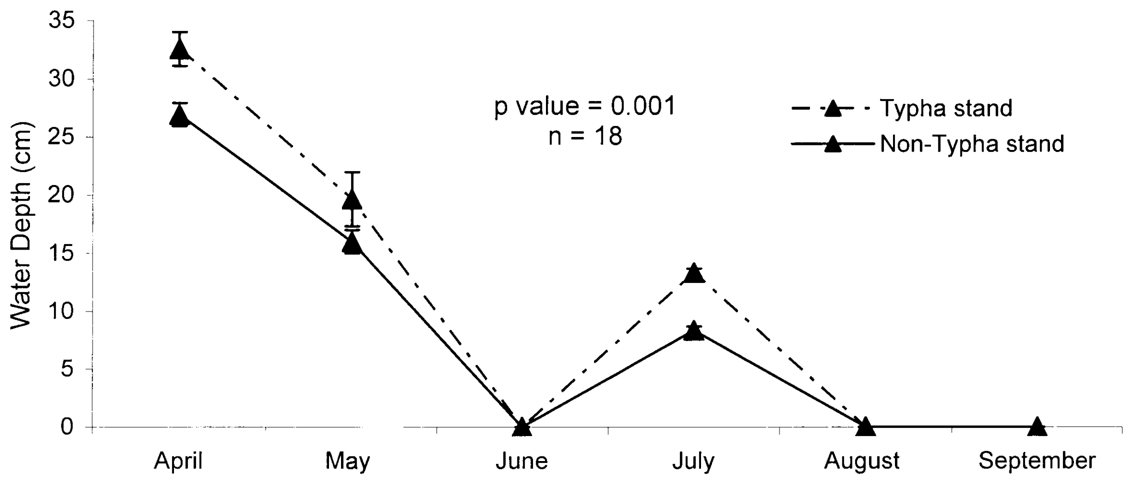


Figure 7b. Mean (± 1 SE) monthly water depth at Suffolk, summer 2007 growing season (April to September).

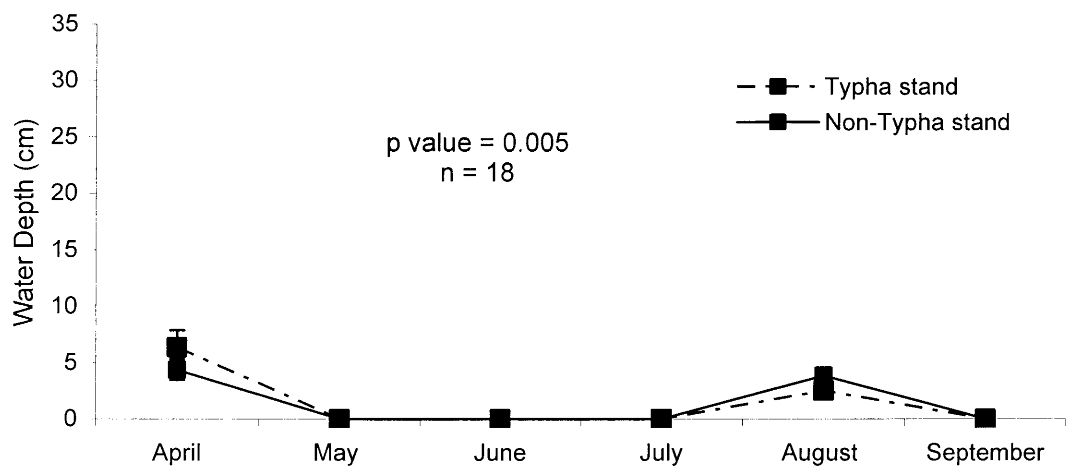


Figure 7c. Mean (± 1 SE) monthly water depth at Courtland East summer 2007 growing season (April to September).

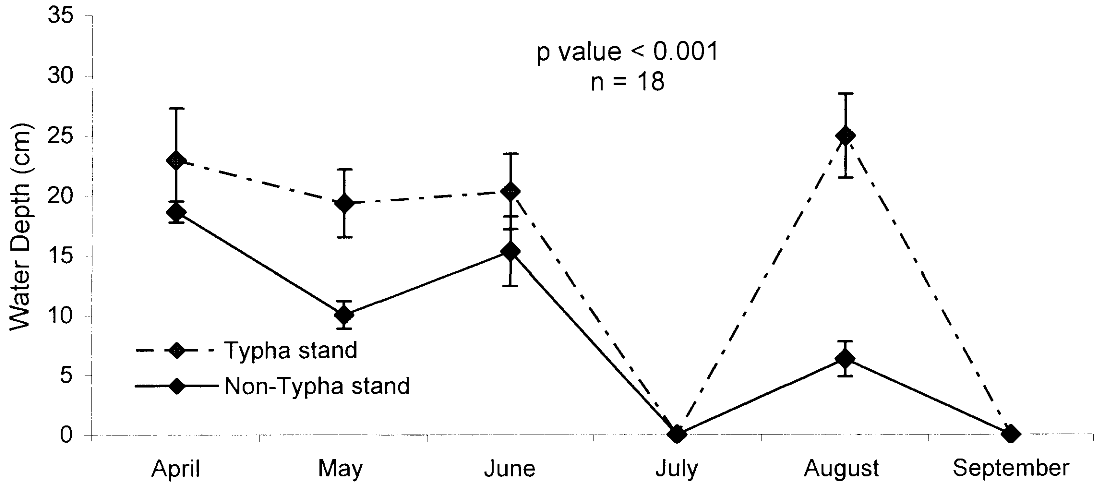


Figure 7d. Mean (± 1 SE) monthly water depth at Courtland West summer 2007 growing season (April to September).

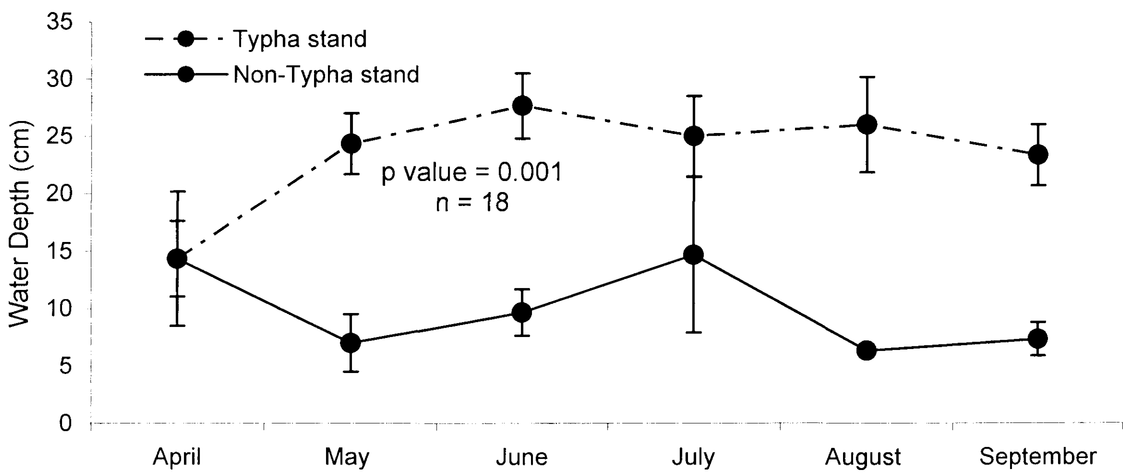


Table 4. Range of water depths, 2007 growing season (April to September)

	Typha stands	Non-*Typha* stands
Sandy Bottom	0 – 33 cm	0 – 28 cm
Suffolk Bypass	0 – 7 cm	0 – 5 cm
Courtland East	0 – 25 cm	0 – 18 cm
Courtland West	14 – 28 cm	7 – 14 cm

Despite significant differences in water depth, all sites were inundated during the growing season for a period of time sufficient to support a prevalence of hydrophytic vegetation (Table 5). In all the stands, wetland indicator species with an indicator status of OBL, FACW, or FAC, made up greater than 80% of the total relative importance value (IV), and there was no significant difference between NT and T stands. Mean weighted average values (WA) (calculated based on weighting the wetland indicator index by IV, Table 5) fall between 1 and 1.5, indicating that the sites are dominated by obligate (OBL) and facultative wet (FACW) species.

Table 5. Summary of total number of species observed, mean (±1 SE) relative importance value of all wetland indicator species (OBL, FACW, and FAC) for each stand, and mean (±1 SE) weighted average over 2007 growing season (April to September).

	Courtland East		Courtland West		Suffolk Bypass		Sandy Bottom	
	Typha	Non-*Typha*	*Typha*	Non-*Typha*	*Typha*	Non-*Typha*	*Typha*	Non-*Typha*
Total Species observed	11	18	17	31	16	17	7	10
Total Importance Value of OBL, FACW, and FAC species	91.61 ±4.27	98.19 ±1.81	88.96 ±2.34	91.56 ±2.78	81.15 ±4.46	90.26 ±3.44	94.28 ±5.72	100.00 ±0
Weighted Average	1.02 ±0.020	1.02 ±0.011	1.22 ±0.029	1.07 ±0.022	1.05 ±0.019	1.03 ±0.037	1.00 ±0	1.00 ±0

Vegetation Communities

Other species besides *Typha* were co-dominant in the T stands in all sites except SB. This showed that, the vegetation at these sites were not monocultures, despite the dense *Typha* growth. Significantly higher peak season aboveground standing crop biomass (SCB) was seen in T stands at CE and SB, while the differences were not significant at SF and CW (Figure 8). The sites where there was no significant difference between the SCB of the T and NT stands (SF and CW) were sites in which emergent perennials such as *Scirpus cyperinus, Juncus effusus,* and *Leersia oryzoides* were dominant in the NT stands (Table 6).

Figure 8. Mean (± 1 SE) peak season standing stock aboveground biomass, 2007, * indicates significant difference between *Typha* and non-*Typha* stands at the same site.

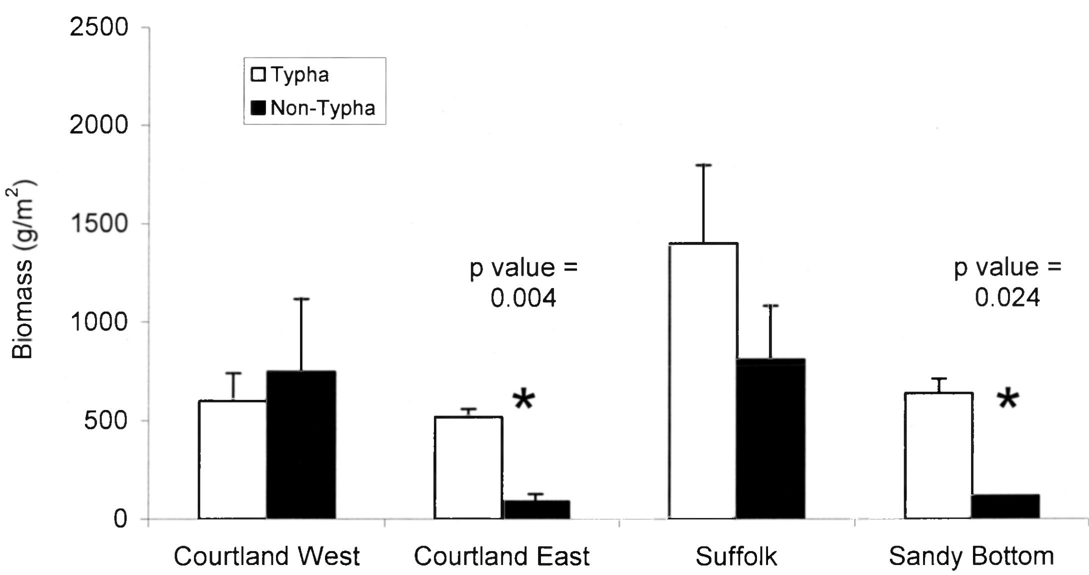


Table 6. Dominant species and relative importance values (IV), determined by the 50/20 Rule (Environmental Lab 1987)

	Typha stands	Non-*Typha* stands
Courtland West	*Hydrocotyle umbellata* (IV 24.59) *Typha* (IV 24.23)	*Hydrocotyle umbellata* (IV 16.79) *Scirpus cyperinus* (IV 13.58) *Juncus effusus* (IV 10.34) *Leersia oryzoides* (IV 7.34)
Courtland East	*Typha* (IV 59.17) *Pontedaria cordata* (IV 20.93)	*Pontedaria cordata* (IV 36.71) *Peltandra virginica* (IV 21.48)
Suffolk Bypass	*Typha* (IV 39.59) *Juncus effusus* (IV 23.98)	*Juncus effusus* (IV 50.96)
Sandy Bottom	*Typha* (IV 58.87)	*Typha* (IV 24.90) *Juncus acuminatus* (IV 14.93) *Eleocharis obtusa* (IV 14.59)

Species richness (SR), and Shannon diversity index (H') for T and NT stands in each site, as well as the Hutcheson modified t-test comparison of H' within each site, are presented in Tables 7 and 8, larger H' indicates higher diversity. CW had significantly higher H' in the T stand, though SR was significantly lower. SF exhibited no significant difference in H' or SR between T and NT stands. SB had higher H' in the NT stand and no difference in SR. There is no clear negative or positive trend associated with H' or SR in T and NT stands. Therefore, it can be concluded that there was no negative effect of dominant *Typha* on the H' or SR at any of the sites.

Table 7. Shannon diversity index (H'), including results of statistical analysis of difference between *Typha* and Non-*Typha* stands, * indicates significant difference in H' between stands at a given site, as indicated by Hutcheson's modified t-test ($\alpha = 0.05$).

Sites	*Typha* Stand Shannon Diversity (H')	Non-*Typha* Stand Shannon Diversity (H')
Courtland West* p value < 0.001	2.28	0.38
Courtland East* p value < 0.001	1.33	2.15
Suffolk	1.91	1.87
Sandy Bottom* p value < 0.001	1.28	2.14

Table 8. Mean species richness (SR) (±1 SE) including results of statistical analysis of difference between *Typha* and Non-*Typha* stands, * indicates significant difference in SR between stands at a given site, as indicated by t-test ($\alpha = 0.05$).

Sites	*Typha* Stand Species Richness (SR)	Non-*Typha* Stand Species Richness (SR)
Courtland West* p value = 0.035	5.67 ±0.45	7.11 ±0.48
Courtland East	3.22 ±0.33	4.17 ±0.57
Suffolk	4.06 ±0.36	3.50 ±0.25
Sandy Bottom	2.22 ±0.19	2.28 ±0.19

Ellenberg Community Coefficient Similarity Index (SI_E) results for T and NT stands within the same sites indicated a strong similarity ($SI_E > 0.50$) which illustrates that while the paired stands are dominated by different species, they are more similar to one another than stands in other sites (Table 9). This indicates that even though the dominant vegetation is different across the site, there is still homogeneity within sites. This supports the conclusion that vegetation communities should be evaluated on a site-by-site basis.

Table 9. Matrix of Ellenberg Community Coefficient Similarity Index (SI_E) values calculated from mean relative IV of species over 2007 growing season (April-September), * indicates similarity between the sites ($SI_E > 0.50$), boxes enclose similarity values for comparisons across sites.

		Sandy Bottom		Suffolk		Courtland West		Courtland East
		Non-*Typha*	*Typha*	Non-*Typha*	*Typha*	Non-*Typha*	*Typha*	Non-*Typha*
Courtland East	*Typha*	0.37	0.46	0.45	0.47	0.36	0.44	0.77*
	Non-*Typha*	0.12	0.29	0.19	0.24	0.39	0.41	
Courtland West	*Typha*	0.20	0.28	0.45	0.47	0.82*		
	Non-*Typha*	0.29	0.28	0.48	0.51*			
Suffolk	*Typha*	0.41	0.36	0.82*				
	Non-*Typha*	0.39	0.21					
Sandy Bottom	*Typha*	0.79*						

The total IV of all perennial species in each site was higher in T stands than NT stands at all sites (Figures 9 and 10). IV of perennial species also increased with age of the site. Based on models of primary succession in created wetlands, the trend of an increase in IV of perennials in older sites is consistent with other models of primary succession in created wetlands.

Figure 9. Proportion of total relative importance values of perennial, annual, and facultative annuals in only *Typha* stands at all study sites, summer 2007 growing season.

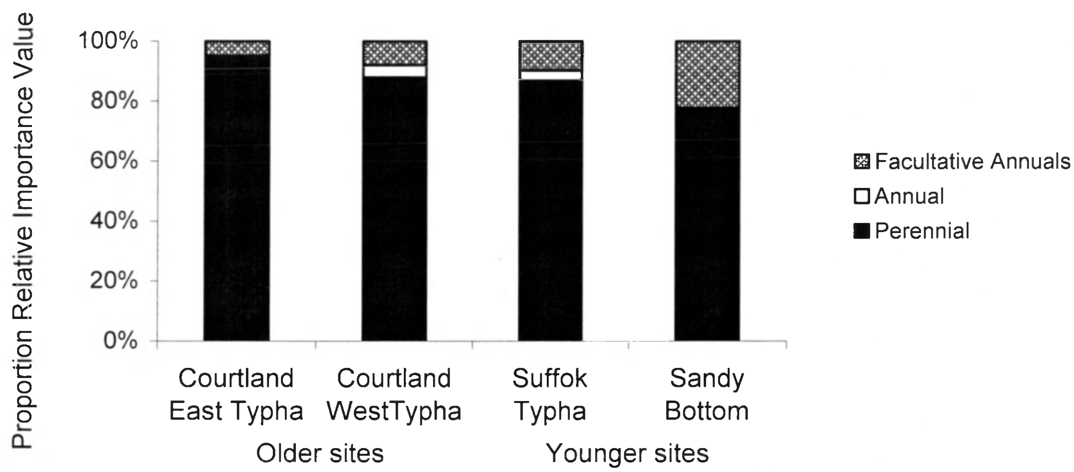


Figure 10. Proportion of total relative importance values of perennial, annual, and facultative annuals in only non-*Typha* stands at all study sites, summer 2007 growing season.

Discussion

Water Depth and Wetland Indicator Status

Initially, when selecting the T and NT stands within each of the sites, I attempted to control for water depth. However, the data indicated that there was a significant difference between monthly water depths in T and NT stands at all the sites (Figures 7a-d). While water depth values were significantly different, they were not different enough to cause significant change in vegetation weighted averages (WA) of the stands, or the proportion of wetland indicator species. Therefore, the wetland systems are considered similar enough to allow a comparison of vegetation community characteristics. The Ellenberg Similarity Index (SI_E) values (Table 9) also showed that within sites the T and NT stands were more similar to one another than to stands in other sites. Based on these results, differences in water depth and dominance by *Typha* did not seem to have any effect on the importance of wetland indicator species in the vegetation community.

Standing Crop Biomass

Peak season standing crop biomass (SCB) ranged from 519-1401 g m^{-2} in the T stands and 88-809 g m^{-2} in the NT stands. The T stands were within the range for natural inland freshwater herbaceous wetlands (500-5500 g m^{-2}) reported by Mitsch and Gosselink (2000). The top of the range for the NT stands was also within this range, but the lower end was not. The higher SCB in the T stands is most likely a factor of the large size of *Typha* aboveground material. The sites with higher SCB in NT stands, CW and SF, were also dominated by large, perennial, prolific plants such as *J. effusus* and *S. cyperinus* that also produce a large amount of aboveground biomass. It was originally hypothesized that T stands would have a significantly higher SCB, than the NT stands within the same sites. This trend was seen in the two sites (CE and SB) where there was a significant difference between SCB. However, SF and CW showed no significant difference in SCB between T and NT stands; these are also the sites in which the NT stands were dominated by large prolific vegetation (*J. effusus* and *S. cyperinus)*. I also hypothesized that there would be a difference in SCB between older and newer sites, but the analysis of variance (ANOVA) (Minitab 15) showed no significant difference in SCB between any of the sites in T or NT stands.

Diversity Indices and Species Richness

While it was part of the sampling design that *Typha* would be a dominant species in the T stands, it was shown that in three of the sites (CW, CE, and SF) other species were co-dominant with *Typha.* This is a strong indication that the occurrence of *Typha* does not limit the growth of other vegetation and that the T stands are not *Typha* monocultures (Table 6). In order to determine if *Typha* dominance is limiting biodiversity I looked at the species richness (SR) and Shannon diversity index (H') for T and NT stands in each site (Zar 1999). The overall H' and SR values seem to indicate that while *Typha* dominance was not positively correlated to increasing diversity at a site, there also does not seem to be a consistent negative effect of high *Typha* density on SR or diversity at any of the sites. Other studies have reported *Typha* invasion and subsequent lowering of species diversity in many types of disturbed wetlands (Newman et al. 1996, Green and Galatowitsch 2001, Woo and Zedler 2002, Childers et al. 2003). However, in this study, no consistent negative effect (decrease in SR or H') was associated with vegetation community dominance by *Typha*. This is most likely due to very low vegetation community diversity that is often observed in all vegetation assemblages in created wetlands (Mitsch and Wilson 1996), therefore the focus needs to be on increasing the diversity throughout the site, not just on removal of *Typha* stands.

The initial experimental design was to group the sites by site age. This type of grouping is not consistent with the vegetation results, as there were no clear patterns in H', SR, or greater similarity, based on Ellenberg Index of Similarity (SI_E), associated with site age. The lack of clear trends associated with newer and older sites indicates that all created mitigation wetlands do not easily fit into successional chronosequences and that inferences made about one wetland often do not translate to other sites of similar age. This is most likely true du e to differences in site construction, especially organic matter amendments, as well as different disturbance regimes.

Community Composition Differences Related to Succession

I analyzed the total importance values (IV) of perennial, annual, and facultative annuals in each stand at each site and compared these results to primary successional models proposed by van der Valk, (1981), Noon (1995), and DeBerry and Perry (2004). The models proposed by van der Valk (1981) and Noon (1995) predict that the proportion of annuals will be high in the first few seasons of primary succession, and then decrease from the time of initial colonization of the site, eventually giving way to a community dominated by perennials. The range for IV of annuals in all the study sites was 0 to 10, which was much lower than predicted by van der Valk and Noon's models, but is consistent with what DeBerry and Perry (2004) found in other southeastern Virginia created wetlands. Despite the lower proportion of annuals than expected in early successional sites, the number of annuals did decrease in the older sites (Figures 9 and 10), which was consistent with the predictions of van der Valk and Noon's previous models of primary succession. The differences seen in the proportion of annuals in the early successional stages at the study sites may be due to the lack of direct surface water connection to other wetlands, which would normally serve as a means of introduction of seeds from annual hydrophytes found in nearby natural wetlands.

Looking at all four sites in the context of Noon's (1995) model, SB and SF can be considered to be in what Noon defined as the Arrival and Establishment Phase (1-4 years since construction). These types of sites would be expected to be dominated by highly competitive quickly reproducing species, generally annuals and prolifically reproducing perennials that utilize "annual-like" strategies (DeBerry and Perry 2005). These species are able to take advantage of large amounts of open soil in newly constructed sites and expand throughout the entire initial growing season via rhizomatous growth, not just when seeds are dispersed. While in Noon's model the very early successional communities exhibited high SR because of recruitment of a wide variety of species, this was not observed at SB and SF, possibly due to the lack of adjacent herbaceous wetlands to serve as propagule sources. Because these sites are not hydrologically connected to other wetlands via surface water, the only opportunity for seeds introduction is through wind-dispersed seeds. Since the majority of wetlands near these sites are mature forested wetlands, the variety of herbaceous wetland propagules is likely lower than if there were adjacent herbaceous wetlands. Therefore, the seeds that do make it into the site are often from the weedy cosmopolitan species, with prolific wind-dispersed propagules, that can be found in ditches and other small confined wet areas. These species include *Typha* spp., *P. australis, S. cyperinus, and J. effusus*. These highly competitive species have the ability to outcompete other vegetation, and combined with the low diversity in introduced propagules, they are quickly able to takeover the early successional sites. The lower recruitment diversity associated with the created wetlands in this study may be a strong control on the successional development of the vegetation community as the sites age.

Noon's model goes on to predict that as herbaceous percent cover increases to 100% or greater, the community shifts from one that is dominated by graminoids, to a forb dominated community. While the percent cover was greater in the older study sites, many of the sites were still dominated by graminoid species such as *Typha* spp., *J. effusus*, and *S. cyperinus*. It is likely that these grass, rush, and sedge dominated communities will persist until woody species such as *Taxodium distichum,* that were planted, and *Salix nigra*, a volunteer, become mature and shade out the herbaceous vegetation layer. Since these created sites were designed to replace the structure and function of palustrine forested wetlands, the mature forested vegetation community is the desired state of these sites, it seems that the successional change, or lack there of, associated with the herbaceous vegetation may not be the most important aspect of the vegetation community development. It is more than likely more important, therefore, to better understand the effect of the entire herbaceous community on the development of woody saplings (Gilliam 2007). Unpublished data collected by Perry and Atkinson (2007) showed that dense *Typha* cover within a 1 m radius of *T. distichum* saplings does not have a negative effect on growth metrics (pers. comm. J. E. Perry).

While some inferences can be made about the vegetation community at these sites in the context of primary successional models, the lack of clear trends associated with newer and older sites indicates that all created mitigation wetlands do not easily fit into successional models and that inferences made about one wetland often do not translate to other sites of similar age.

CHAPTER 4: NUTRIENT AVAILABILITY COMPARISONS

SOIL RESULTS

Soil Organic Matter

There was no significant difference in percent soil organic matter (OM) between T and NT stands within any sites. However, there were significant differences between the sites. Tukey's Honestly Significant Difference (HSD) test was used to determine which sites were significantly different; the results of all repeated measures ANOVA comparisons of soil parameters between sites can be seen in Tables 11 and 12. In 2006, Suffolk (SF) had significantly higher OM than either Courtland East (CE) or Courtland West (CW) (Figure 11). While the differences are not significant in 2007, SF again appears to have higher OM. (Figure 12). The measurements of percent OM for T and NT stands in all sites were statistically similar.

Figure 11. Mean (± 1 SE) percent soil organic matter in *Typha* and non-*Typha* stands, at all study sites, 2006 growing season (June to September).

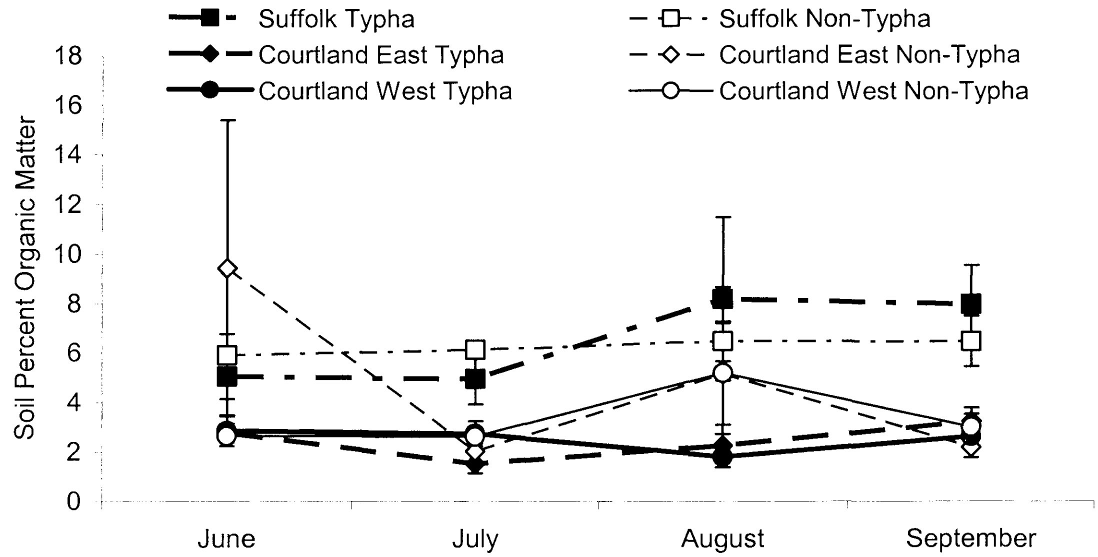
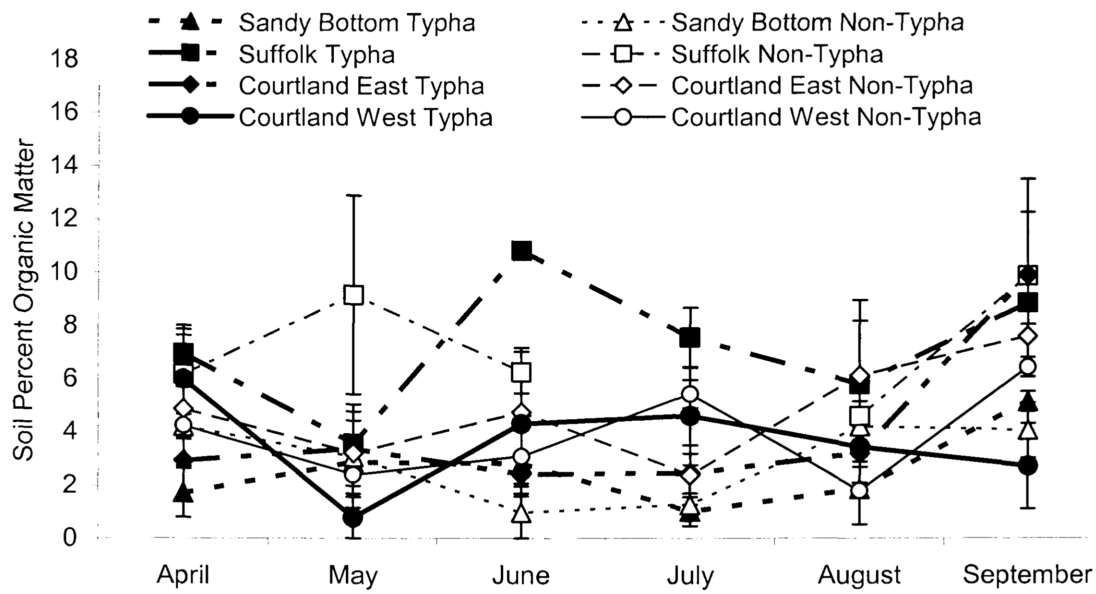


Figure 12. Mean (± 1 SE) percent soil organic matter in *Typha* and non-*Typha* stands, at all study sites, 2007 growing season (April to September).



Soil Total Carbon

There was no significant difference in total carbon (TC) between T and NT stands at SF and CE in 2006. However, TC was significantly higher in the NT stand at CW. There were also significant differences between the sites (Table 11). As was the case with OM in 2006, the soil percent TC was significantly higher at SF than the other two sites. In 2007, SF also had significantly higher percent TC (Table 12), despite there not being a significant difference in soil OM.

In 2007, TC was significantly higher in NT stands at both SF and CE, but no significant differences were seen at Sandy Bottom (SB) and CW. The TC at Suffolk was significantly higher than all other sites (Table 12).

Figure 13. Mean (± 1 SE) soil total carbon in *Typha* and non-*Typha* stands, at all study sites, 2006 growing season (June to September).

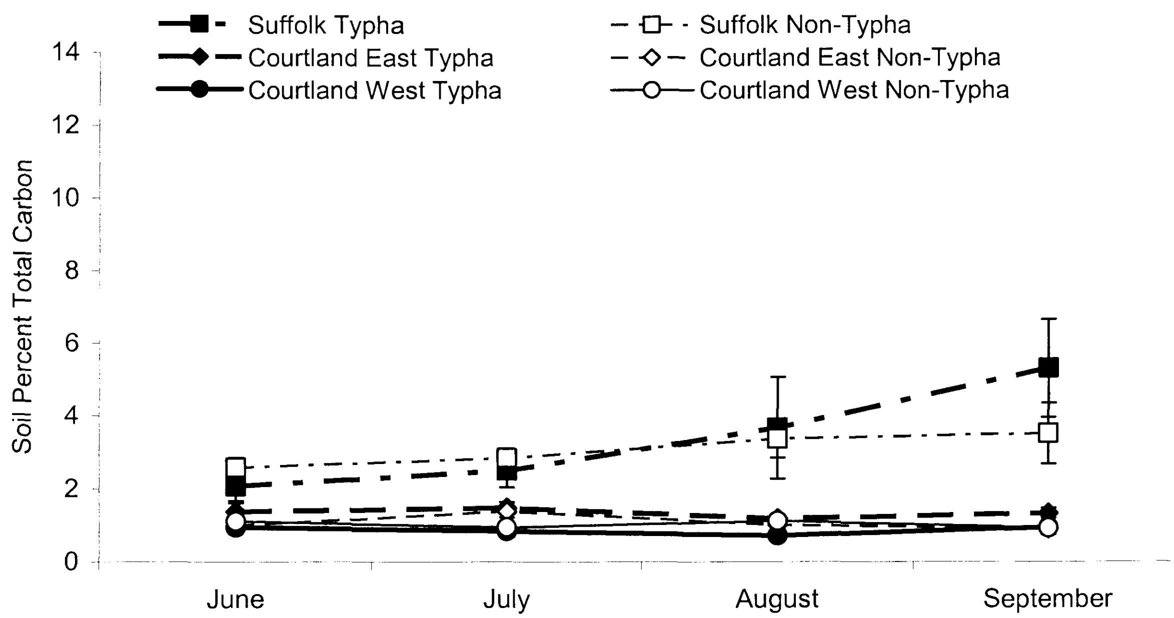
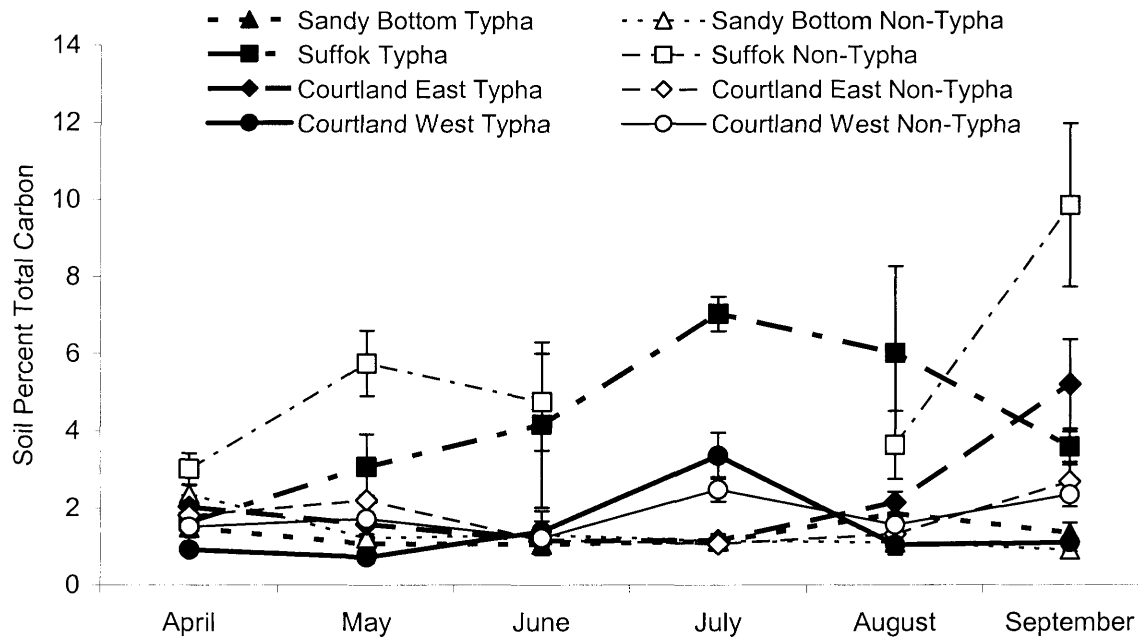


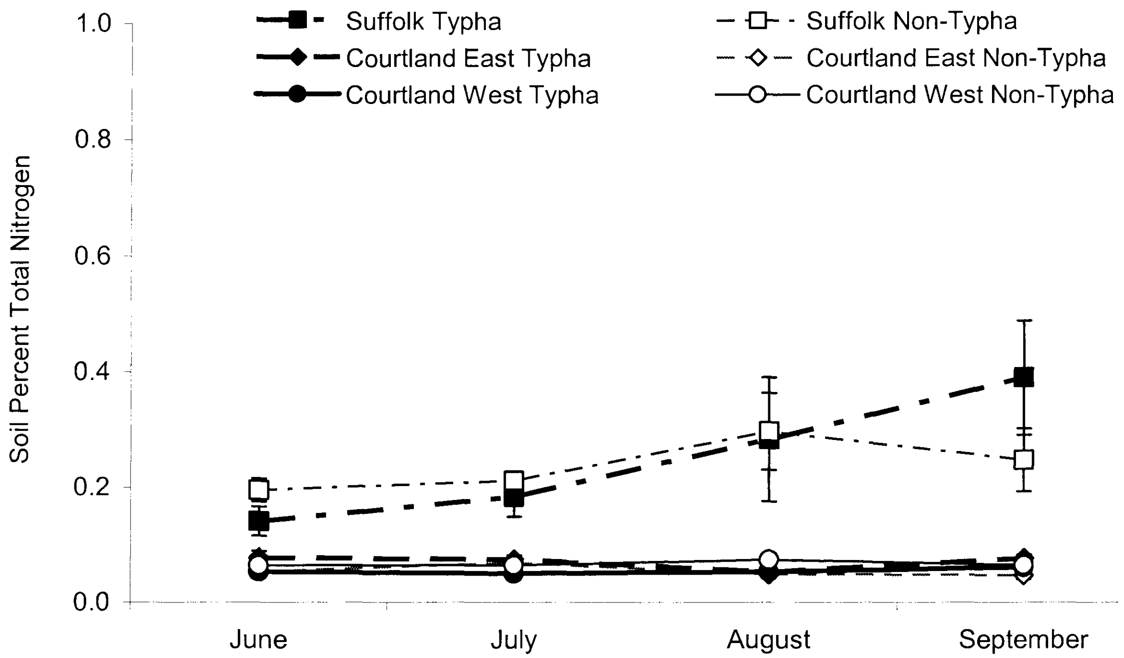
Figure 14. Mean (± 1 SE) soil total carbon in *Typha* and non-*Typha* stands, all study sites, 2007 growing season (April to September).



Soil Total Nitrogen

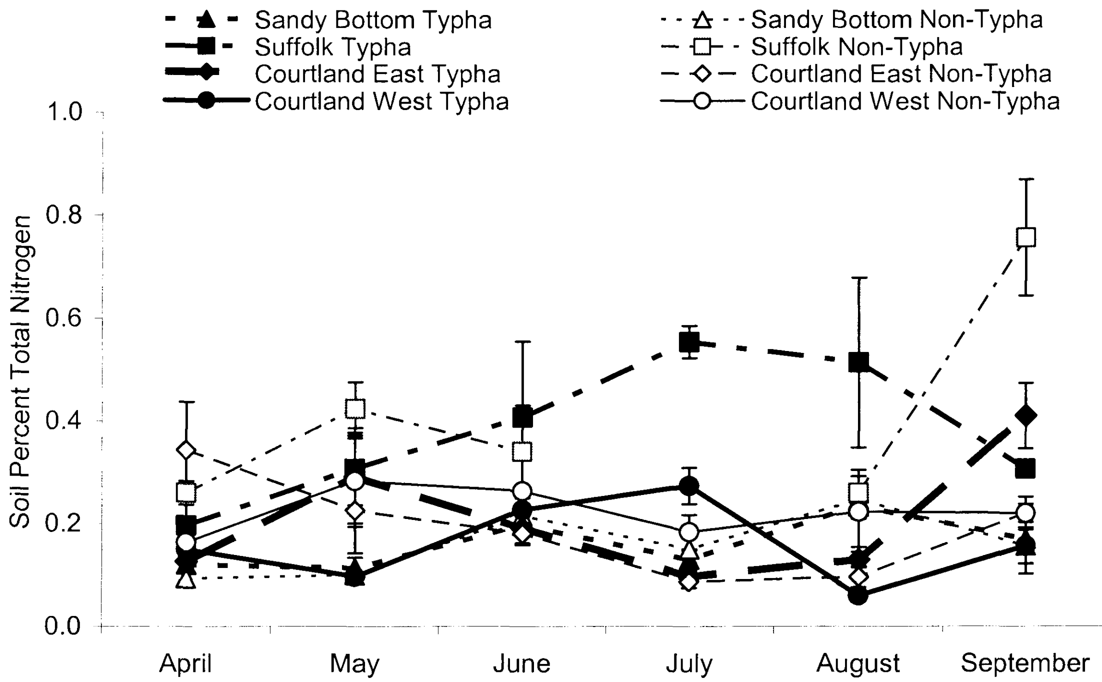
In 2006, the soil total nitrogen (TN) was significantly higher in the T stand at CW, and in the NT stand at CE. No significant differences between T and NT stands were seen at SF. Figure 15 clearly shows the significantly higher TN in both T and NT at SF. There was no significant difference between CE and CW (Table 11).

Figure 15. Mean (± 1 SE) soil total nitrogen in *Typha* and non-*Typha* stands, all study sites, 2006 growing season (June to September).



In 2007, there were differences between sites, with SF having significantly higher TN than all the other sites (Table 12). The opposite trend in TN was observed at CW, where TN was significantly higher in the NT stand; CE showed no significant difference. SB and SF also showed no significant differences between T and NT stands (Figure 16).

Figure 16. Mean (± 1 SE) soil total nitrogen in *Typha* and non-*Typha* stands, all study sites, 2007 growing season (April to September).



At SF the OM, TC, and TN all increased throughout the growing season in 2006, returned to lower levels the following spring, and then increased again throughout the growing season in 2007.

Soil Carbon to Nitrogen Ratio

There was no significant difference in carbon to nitrogen ratio (C:N) in T and NT stands at any sites in 2006 or 2007. There were significant differences in C:N between sites in 2006 (Table 11), but no significant differences were seen between any of the sites in 2007.

Figure 17. Mean (± 1 SE) soil carbon to nitrogen ratio in *Typha* and non-*Typha* stands, all study sites, 2006 growing season (June to September).

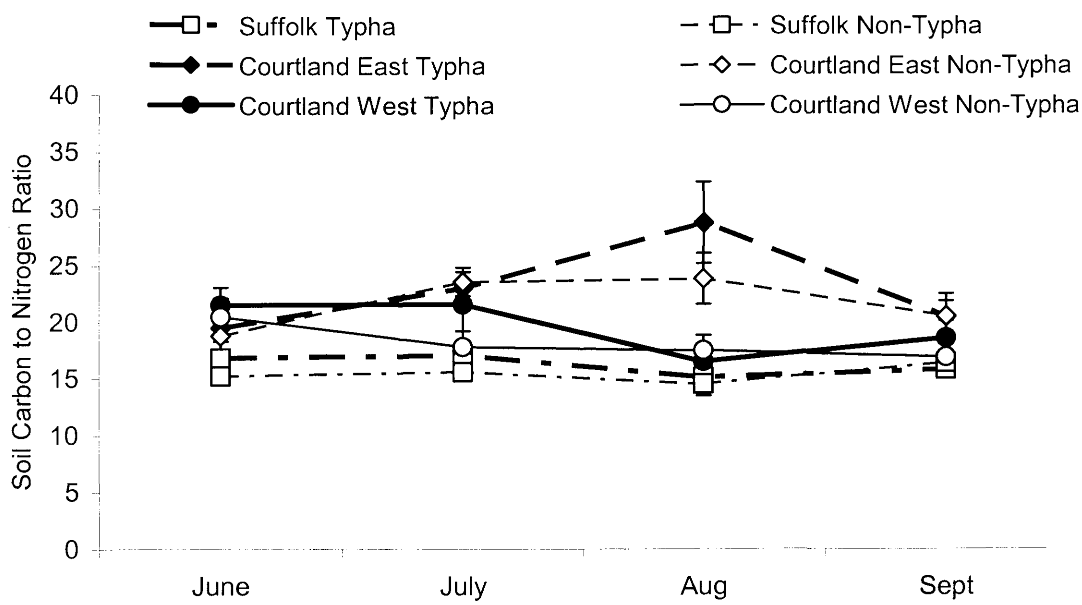
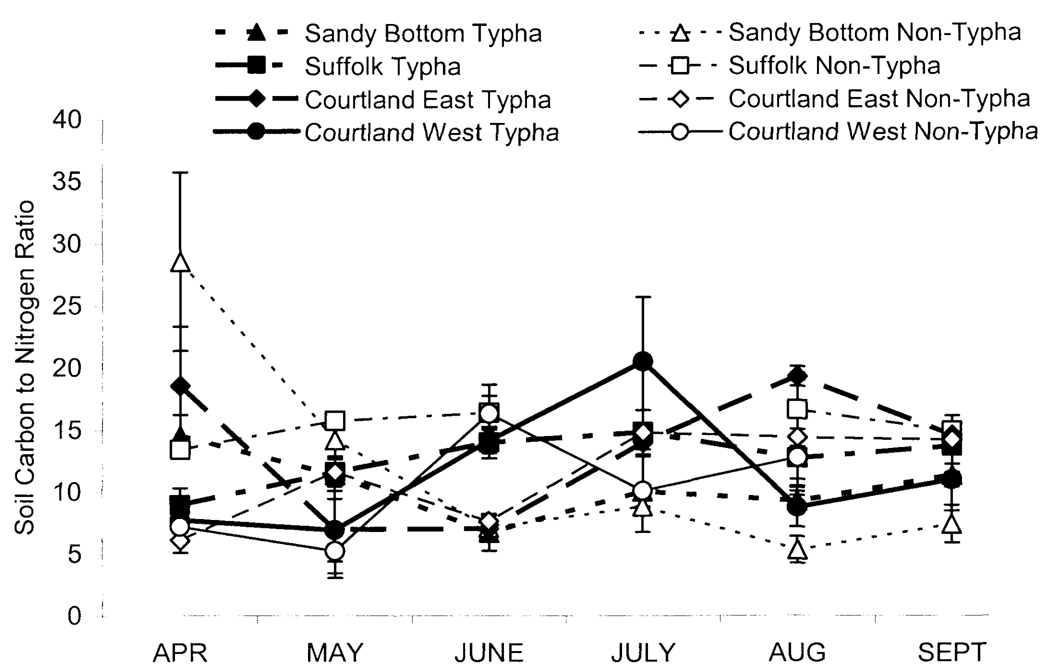
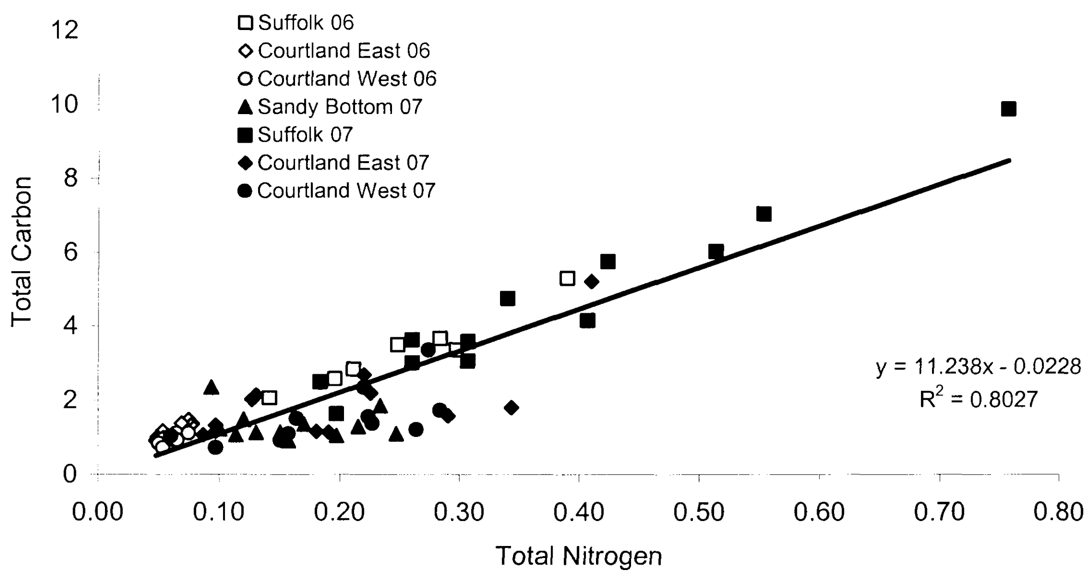


Figure 18. Mean (± 1 SE) carbon to nitrogen ratio in *Typha* and non-*Typha* stands, all study sites, 2007 growing season (April to September).



The scatter plot of soil TC and TN values shows a very tight relationship between soil TC and TN (Figure 19). This is what would be expected, because the majority of soil N is stored as organic material. Based on the slope of the best fit line for 2006 and 2007 combined, the mean overall soil molar N:P ratio in all the sites is 13.04.

Figure 19. Plot of soil total carbon and total nitrogen in *Typha* and non-*Typha* stands, all study sites, 2006 and 2007.



Soil Total Phosphorus

In 2006, none of the sites exhibited a significant difference in soil total phosphorus (TP) between T and NT stands. Repeated measures ANOVA indicated a significant difference between sites, with SF having higher TP in 2006 (Table 11) and again in 2007. However, the 2007 range of mean values (0.025- 0.05%) were less than observed in 2006 (0.05-0.11%). In 2007, TP was significantly higher in NT stands at CW, but no significant differences were measured at SB, SF, and CE (Table 12). An extremely large shift in the baseline of TP is observed from 2006 and 2007, while ecological factors can result in loss of soil TP, this is an extremely large shift in one year, and may indicate inconsistencies in sample collection or analysis.

Figure 20. Mean (± 1 SE) soil percent total phosphorus in *Typha* and non-*Typha* stands, all study sites, 2006 growing season (June to September).

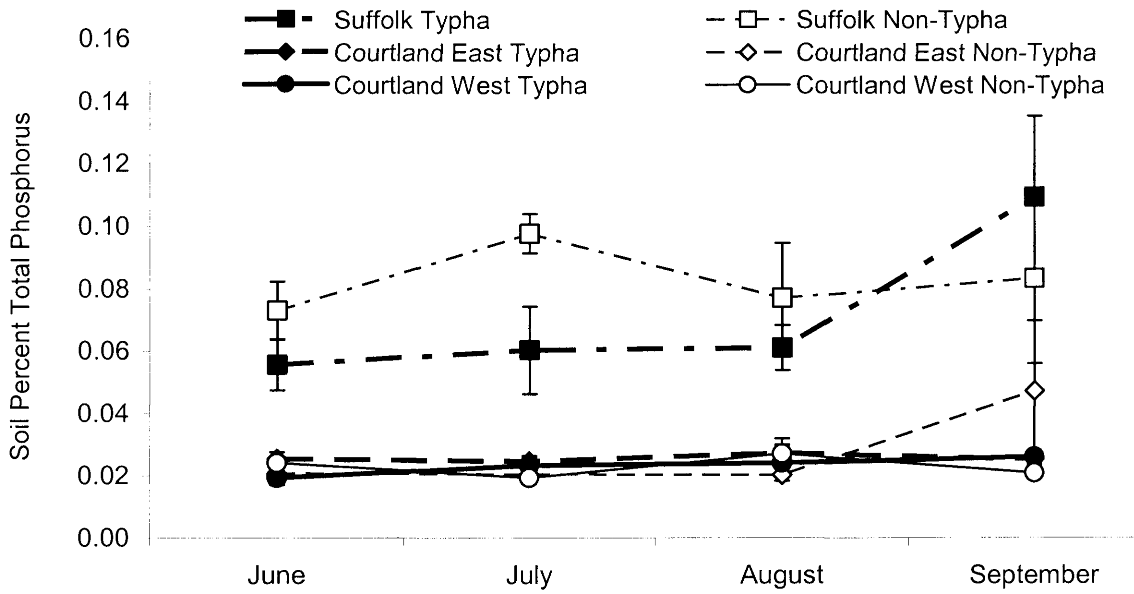
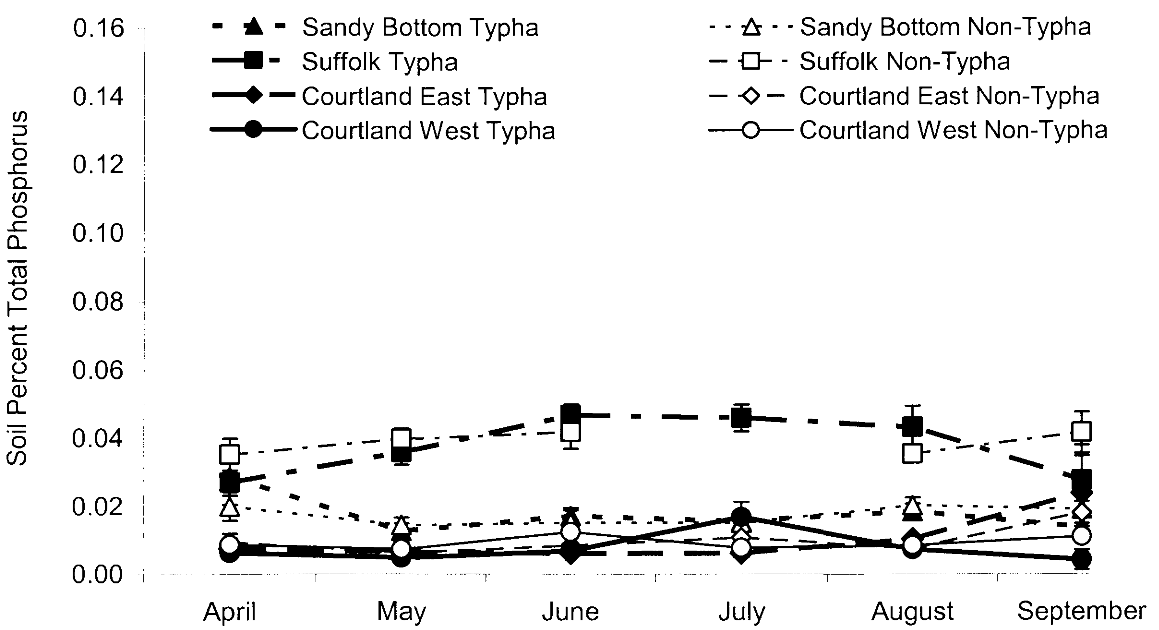
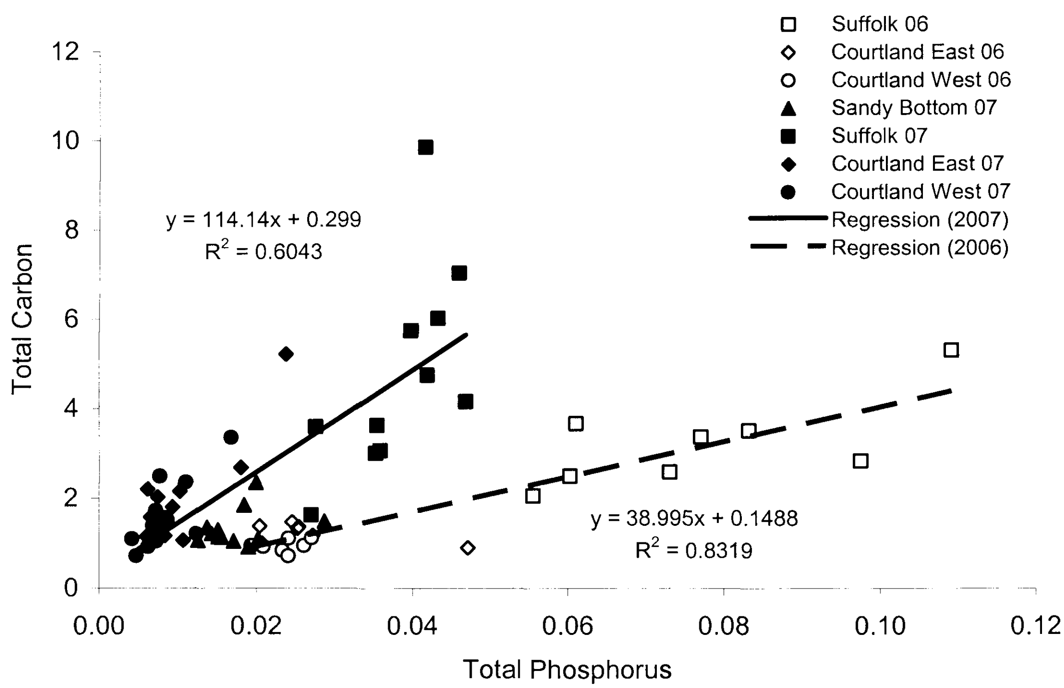


Figure 21. Mean (± 1 SE) soil percent total phosphorus in *Typha* and non-*Typha* stands, all study sites, 2007 growing season (April to September).



The scatter plot of soil TC and TP values does not show a tight relationship (Figure 22); this is because a large amount of soil TP is stored in inorganic forms and so is not closely allied with TC. The difference in C:P ratios between 2006 and 2007 can be clearly seen in Figure 22, a similar trend was observed for soil N:P ratio (Figure 29). The large shift in C:P ratio is driven primarily by the change in TP though there is also a shift to slightly higher TC in 2007.

Figure 22. Plot of soil total carbon and total phosphorus in *Typha* and non-*Typha* stands, all study sites, 2006 and 2007.



Soil Acid Extractable Phosphorus

In 2006, no significant differences in acid extractable phosphorus (AEP) were observed between T and NT stands within any sites. SF had significantly higher AEP than all other sites in 2006 and 2007 (Tables 11 and 12). The AEP results from both 2006 (Figure 23) and 2007 (Figure 24) followed the same trend as the TP for those years (Figures 20 and 21). This indicated that the majority of TP that was measured was composed of AEP. Significant differences in AEP were observed between T and NT stands at CE, but no differences between stands were seen at SB, SF, or SW.

Figure 23. Mean (± 1 SE) percent acid extractable soil phosphorus in *Typha* and non-*Typha* stands, all study sites, 2006 growing season (June to September).

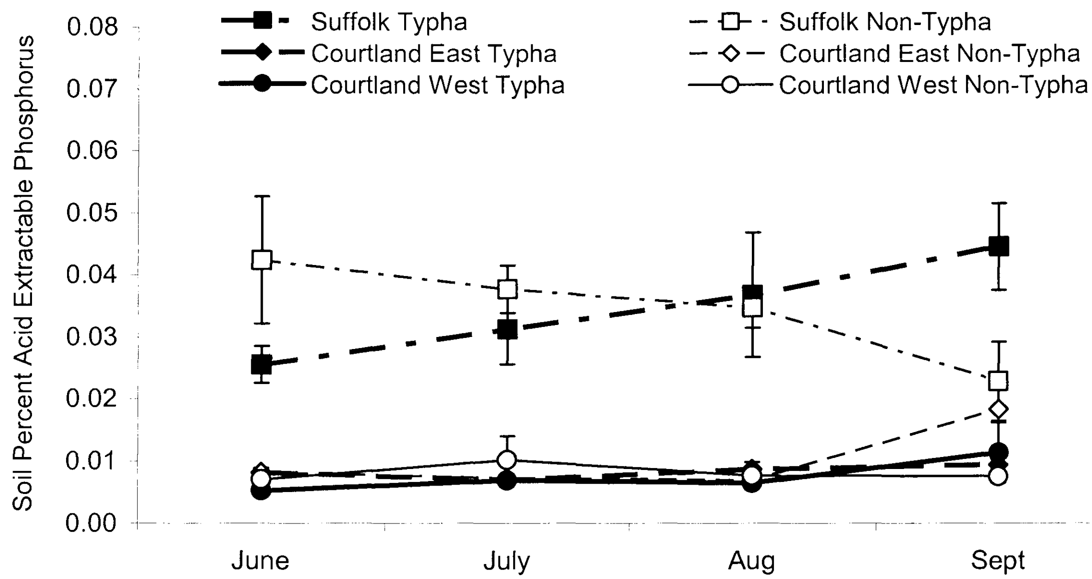
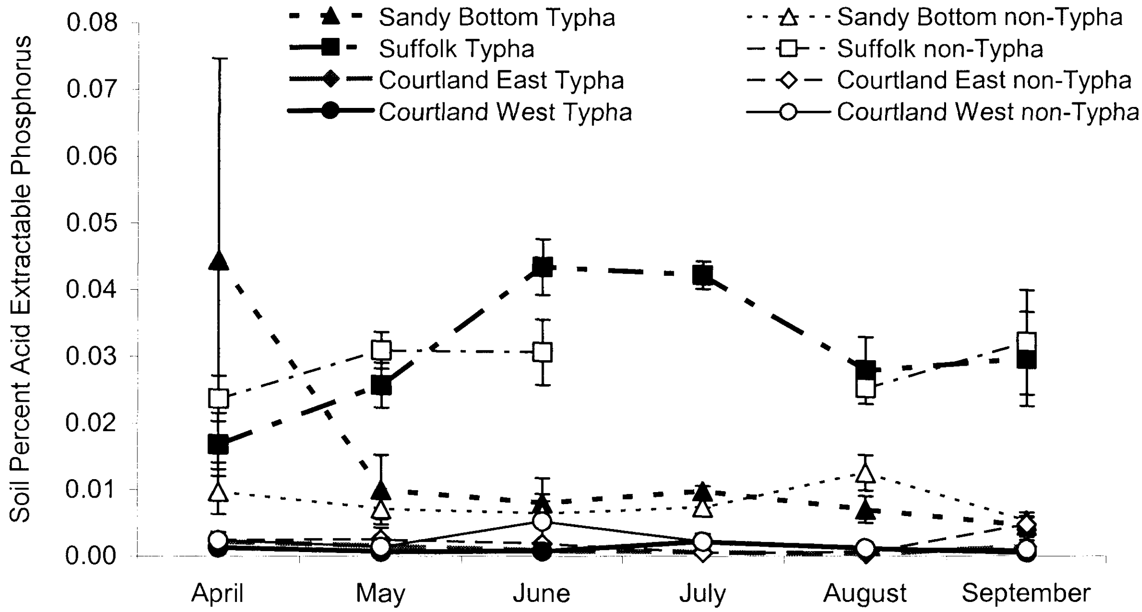


Figure 24. Mean (± 1 SE) percent acid extractable soil phosphorus in *Typha* and non-*Typha* stands, all study sites, 2007 growing season (April to September).



Soil Organic Phosphorus

In 2006 and 2007, there were no significant differences in percent organic phosphorus (OrgP) between T and NT stands within any sites. There were also no significant differences between sites in either year, however there seemed to be a trend of higher OrgP at SF in 2006 (Figure 25) this trend was not seen in 2007 (Figure 26). There are large changes in soil OrgP measured between 2006 and 2007, this extremely large change may again indicate a problem with sample collection or analysis.

Figure 25. Mean (± 1 SE) percent organic soil phosphorus in *Typha* and non-*Typha* stands, all study sites, 2006 growing season (June to September).

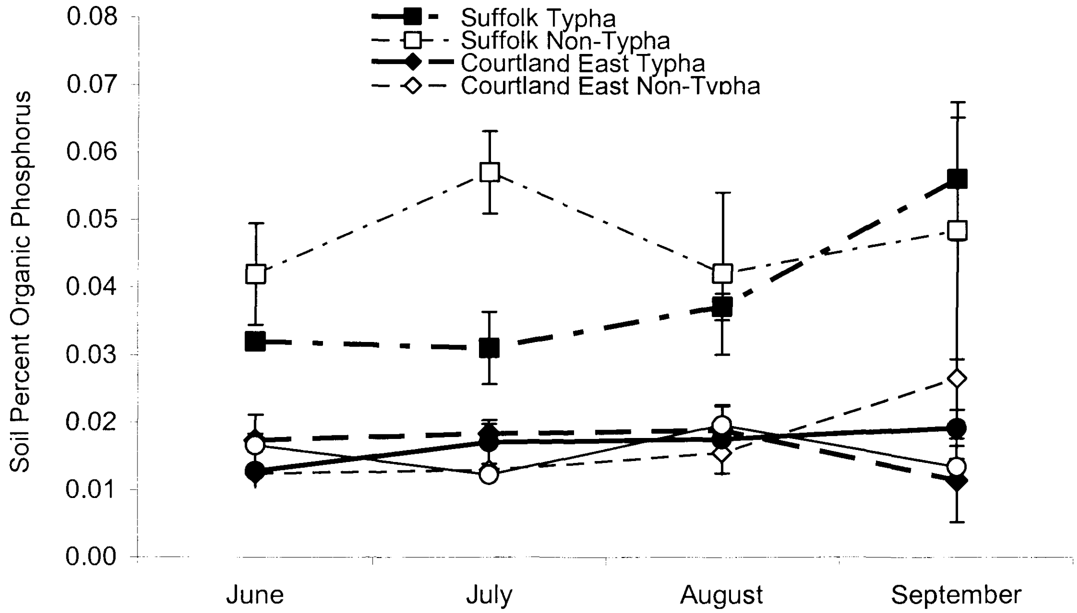
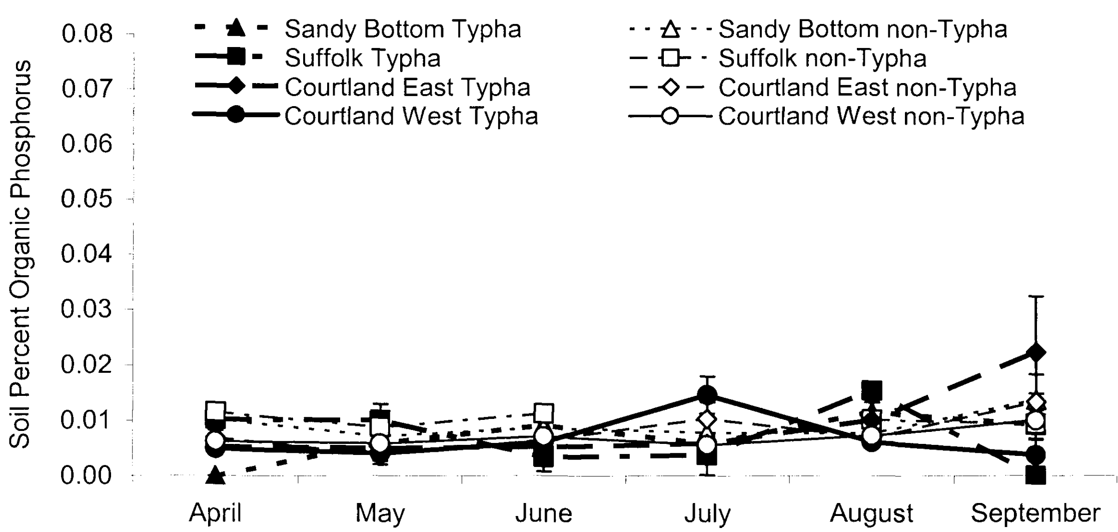


Figure 26. Mean (± 1 SE) percent organic soil phosphorus in *Typha* and non-*Typha* stands, all study sites, 2007 growing season (April to September).



Soil Nitrogen to Phosphorus Ratio

In 2006, the repeated measures ANOVA showed the mean soil N:P ratio was higher in NT stands at CE and CW (Table 10), no significant difference between NT and

T was seen at SF. There were significant differences between SF, CE, and CW (Table 11). In 2007, no significant differences in soil N:P ratios were observed between T and NT stands within any sites. There was a significant difference in N:P ratio between sites (Table 12), with SB and SF exhibiting much lower N:P ratios, especially in the first three months of the growing season (Figure 27). The N:P ratios were much larger in 2007 than 2006, this was especially apparent at CW and SF, where the N:P ratios were an order of magnitude larger. The large change in N:P ratio is caused by the increase in TN and the large decrease in TP, that was observed at all sites from 2006 to 2007. As I have already said this may be due to errors in sampling or analysis, however there are also ecological factors that may lead to decreases in soil TP, that I will discuss further, later in this manuscript.

Figure 27. Mean (± 1 SE) soil nitrogen to phosphorus ratio in *Typha* and non-*Typha* stands, all study sites, 2006 growing season (June to September).

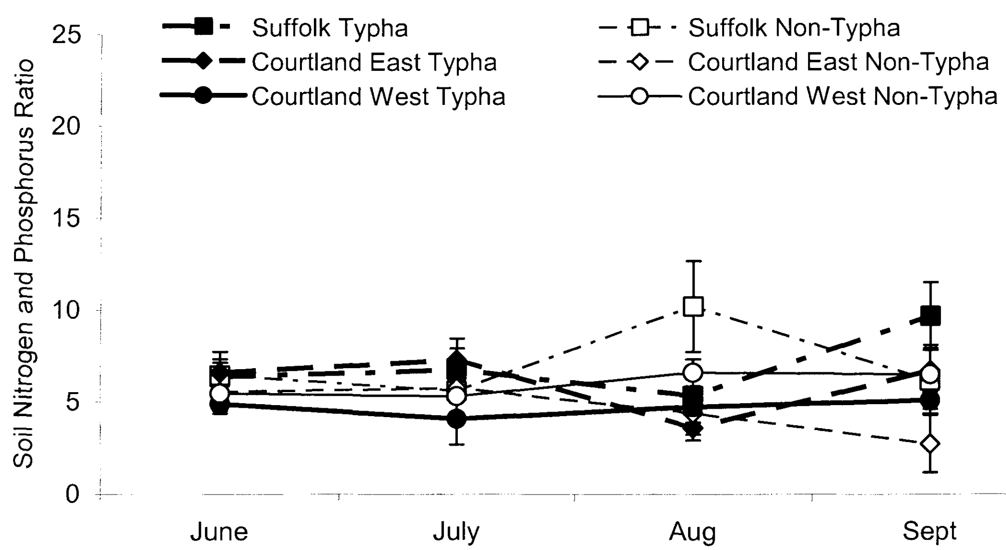
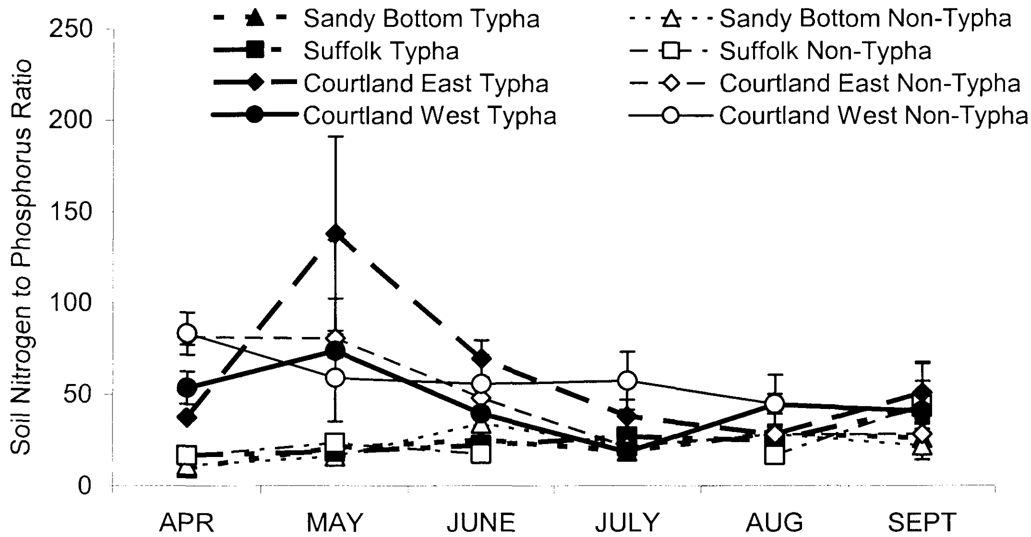
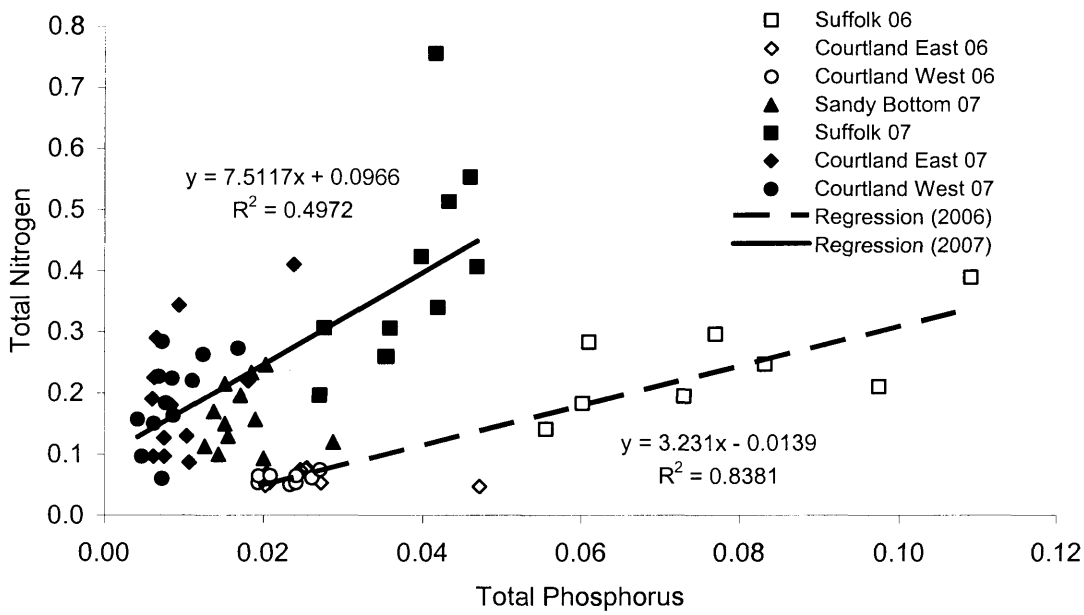


Figure 28. Mean (± 1 SE) nitrogen to phosphorus ratio in *Typha* and non-*Typha* stands, all study sites, 2007 growing season (April to September).



The scatter plot of soil TP and TN values does not show a tight relationship. This is caused by the large changes in TN and TP between 2006 and 2007 and can be seen in the shift from a low slope (3.23) in 2006 to a higher slope (7.51) in 2007 (Figure 29). This change in slope may indicate successional changes in the soil nutrient availabilities at all the sites or a problem in sampling techniques between 2006 and 2007. The higher N:P ratio in 2007 is not completely controlled by TP, there is also an increase in soil TN that contributed to the higher ratio.

Figure 29. Plot of soil total nitrogen and total phosphorus in *Typha* and non-*Typha* stands, all study sites, 2006 and 2007.



Soil Summary

Table 10. Summary of the results of Repeated Measures ANOVA ($\alpha = 0.05$) comparison of soil parameters between *Typha* and non-*Typha* stands.

	Typha and non-*Typha* stand comparisons within study sites	
	2006	2007
Organic Matter	No difference at any sites	No difference at any sites
Total Carbon	NT significantly higher at CW No difference at SF or CE	NT significantly higher at SF and CE No difference at CW or SB
Total Nitrogen	T significantly higher at CW NT significantly higher at CE No difference at SF	NT significantly higher at CW No difference at SF, SB, or CE
Total Phosphorus	No difference at any sites	NT significantly higher at CW No difference at SF, SB, or CE
Acid Extractable Phosphorus	No difference at any sites	NT significantly higher at CE No difference at SF, SB, or CW
Organic Phosphorus	No difference at any sites	No difference at any sites
Nitrogen to Phosphorus Ratio	T significantly higher at CE NT significantly higher at CW No difference at SF	No difference at any sites
Carbon to Nitrogen Ratio	No difference at any sites	No difference at any sites

Table 11. Summary of mean soil parameters (± 1 SE) for each site, combined T and NT, summer 2006. Different letters indicate significant differences ($p < 0.05$) between sites.

2006	Suffolk	Courtland East	Courtland West
Organic Matter	6.4 (± 0.42) ^{a}	3.58 (± 0.92) ^{b}	2.94 (± 0.35) ^{b}
Total Carbon	3.23 (± 0.35) ^{a}	1.20 (± 0.07) ^{b}	0.94 (± 0.04) ^{b}
Total Nitrogen	0.24 (± 0.028) ^{a}	0.063 (± 4.6 E $^{-3}$) ^{b}	0.061 (± 0.029) ^{b}
Total Phosphorus	0.077 (± 6.7 E $^{-3}$) ^{a}	0.026 (± 3.1 E $^{-3}$) ^{b}	0.023 (± 1.0 E $^{-3}$) ^{ba}
Acid Extractable Phosphorus	0.035 (± 2.7 E $^{-3}$) ^{a}	9.2 E $^{-3}$ (± 1.3 E $^{-3}$) ^{b}	7.8 E $^{-3}$ (± 7.0 E $^{-4}$) ^{b}
Organic Phosphorus	0.043 (± 3.5 E $^{-3}$) ^{a}	0.017 (± 1.7 E $^{-3}$) ^{a}	0.016 (± 1.0 E $^{-3}$) ^{a}
Nitrogen to Phosphorus Ratio	7.06 (± 0.65) ^{a}	5.33 (± 0.57) ^{b}	5.3 (± 0.30) ^{b}
Carbon to Nitrogen Ratio	15.8 (± 0.31) ^{a}	22.2 (± 1.13) ^{b}	18.8 (± 0.73) ^{c}

Large annual variation is observed across a variety of parameters and at all three sites sampled in 2006 and 2007 (Table 13). Therefore, it would indicate that it is either an artifact of an error in sampling collection, or is related to environmental factors such as climatic controls or biogeochemical processes occurring at the study sites. There is no way to tell form these data whether this is an artifact of sampling error or reflects the annual changes that are occurring at the study sites, without conducting another year of sampling.

Table 12. Summary of mean soil parameters (± 1 SE) for each site, combined T and NT, summer 2007. Different letters indicate significant differences ($p < 0.05$) between sites.

2007	Sandy Bottom	Suffolk	Courtland East	Courtland West
Organic Matter	2.75 (± 0.41) [a]	7.15 (± 0.62) [a]	4.41 (± 0.68) [a]	3.76 (±0.50) [a]
Total Carbon	1.33 (± 0.12) [a]	4.63 (± 0.65) [b]	1.614 (± 0.33) [c]	1.96 (± 0.33) [a]
Total Nitrogen	0.16 (± 0.015) [a]	0.40 (± 0.049) [b]	0.20 (± 0.30) [c]	0.19 (± 0.02) [a]
Total Phosphorus	0.017 (± 1.2 E^{-3}) [a]	0.038 (± 2.0 E^{-3}) [b]	0.01 (± 1.0 E^{-3}) [ac]	8.0 E^{-3} (± 1.0 E^{-3}) [c]
Acid Extractable Phosphorus	0.011 (± 3.1 E^{-3}) [a]	0.031 (± 2.5 E^{-3}) [b]	2.0 E^{-3} (± 3.6 E^{-4}) [c]	2.0 E^{-3} (± 3.7 E^{-4}) [c]
Organic Phosphorus	8.0 E^{-3} (± 9.8 E^{-4}) [a]	9.0 E^{-3} (± 1.3 E^{-4}) [a]	8.0 E^{-3} (± 1.4 E^{-3}) [a]	7.0 E^{-3} (± 8.5 E^{-4}) [a]
Nitrogen to Phosphorus Ratio	21.9 (± 2.3) [a]	24.5 (± 2.45) [ab]	54.1 (± 5.5) [c]	52.1 (± 2.3) [bc]
Carbon to Nitrogen Ratio	11.2 (± 1.6) [ac]	13.9 (± 0.75) [b]	12.4 (± 1.1) [c]	10.7 (± 1.6) [da]

Table 13. Summary of changes in mean soil parameters for each site, reported as change in percent of bulk soil, combined T and NT, from 2006 to 2007.

	Suffolk	Courtland East	Courtland West
Organic Matter	Increases 1%	Increases 1%	Increases 1%
Total Carbon	Increases 1%	Increases 0.5%	Increases 1%
Total Nitrogen	Increases 0.2%	Increase 0.15%	Increases 0.15%
Total Phosphorus	Decreases 0.03%	Decreases 0.015%	Decreases 0.015%
Acid Extractable Phosphorus	Stays same	Decreases 7.0 E $^{-3}$%	Decreases 6.0 E $^{-3}$%
Organic Phosphorus	Decreases 0.035%	Decreases 0.01%	Decreases 0.01%
Nitrogen to Phosphorus Ratio	Increases 3 times	Increases 10 times	Increases 10 times
Carbon to Nitrogen Ratio	Decreases 0.8 times	Decreases 0.55 times	Decreases 0.55 times

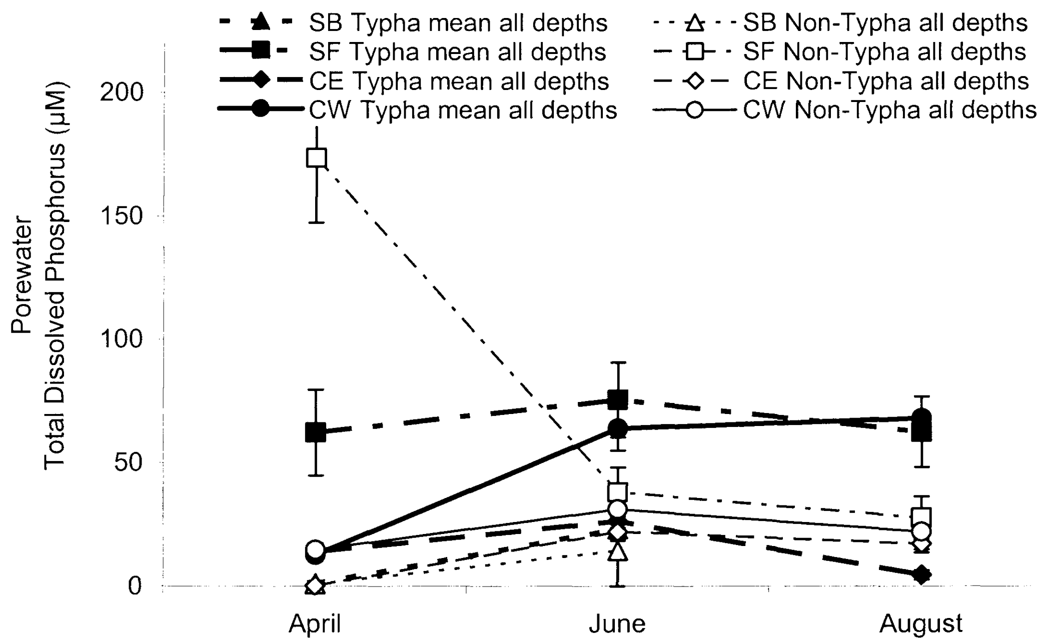
POREWATER RESULTS

While there was some variability the overall porewater nutrient concentrations over the 20 cm sampling interval were not consistently different (Figures 34-37). Therefore, the mean value for the top 20 cm of soil was used for statistical comparisons between sites.

Porewater Total Dissolved Phosphorus

Significant differences in total dissolved phosphorus (TDP) were observed between T and NT stands at CW. However, no significant differences were seen at SB, SF, and CE. SF had significantly higher TDP than all other sites (Table 15). This is most likely due to the very high NT TDP that was measured in April, the porewater DOP decreased in July and August (Figure 30). This same pattern was seen in dissolved inorganic phosphorus (DIP) and dissolved organic phosphorus (DOP) (Figures 31 and 32).

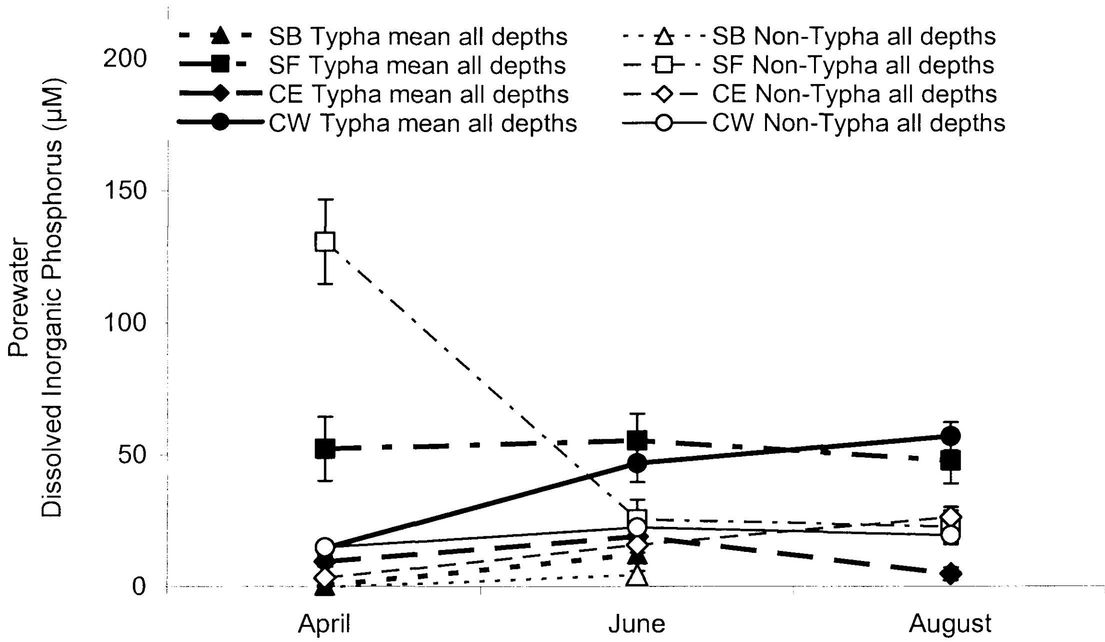
Figure 30. Mean (± 1 SE) bimonthly porewater total dissolved phosphorus in *Typha* and non-*Typha* stands, values are mean of top 20 cm of soil, for all study sites, 2007 growing season (April to August).



Porewater Dissolved Inorganic Phosphorus

Significant differences in dissolved inorganic phosphorus (DIP) were observed between T and NT stands at SB and CW, but no significant differences were seen at SF and CE. However, SF was again significantly higher with a mean of (56.39 µM), almost twice CW (32.43 µM), the next highest site (Table 15). The majority of the TDP at all sites is composed of DIP.

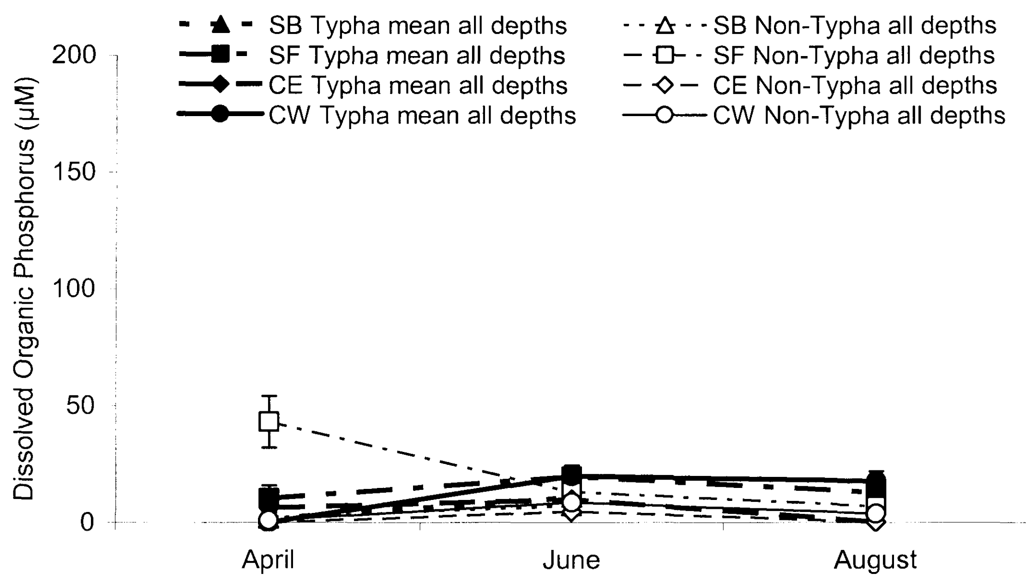
Figure 31. Mean (± 1 SE) bimonthly porewater dissolved inorganic phosphorus in *Typha* and non-*Typha* stands, values are mean of top 20 cm of soil, for all study sites, 2007 growing season (April to August).



<u>Porewater Dissolved Organic Phosphorus</u>

All sites had significantly higher dissolved organic phosphorus (DOP) in T stands, except SF, which had no significant difference between T and NT. The DOP at SF was again higher than all other sites and twice as high as the next highest site, CW (Table 15).

Figure 32. Mean (± 1 SE) bimonthly porewater dissolved organic phosphorus in *Typha* and non-*Typha* stands, values are mean of top 20 cm of soil, for all study sites, 2007 growing season (April to August).



Porewater Ammonium

A significant difference in ammonium (NH_4^+) concentration was observed between T and NT stands at SB, but there were no significant differences between T and NT were seen at SF, CE, and CW. This is opposite of the trend for all forms of P; CW has highest NH_4^+ and SF has the lowest, though it was not significantly different from CE and SB (Figure 33).

Figure 33. Mean (± 1 SE) bimonthly porewater ammonium in *Typha* and non-*Typha* stands, values are mean of top 20 cm of soil, for all study sites, 2007 growing season (April to August).

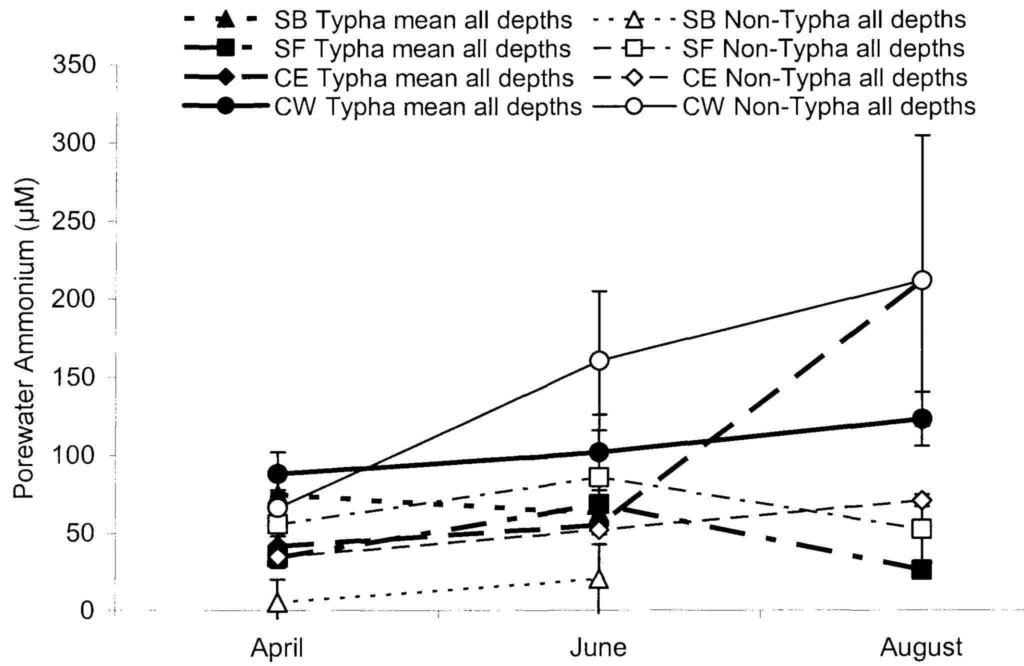


Table 14. Summary of the results of Repeated Measures ANOVA ($\alpha = 0.05$) comparison of porewater nutrient concentrations between *Typha* and non-*Typha* stands.

Typha and non-*Typha* stand comparisons within study sites

Total Dissolved Phosphorus	T stand significantly higher at CW No difference at SB, SF, or CE
Dissolved Inorganic Phosphorus	T stand significantly higher at CW and SB No difference at SF or CE
Dissolved Organic Phosphorus	T stand significantly higher at CE, CW, and SB No difference at SF
Ammonium	T stand significantly higher at SB No difference at SF, CE, or CW

Table 15. Summary of mean porewater parameters (± 1 SE) for each site, combined T and NT, summer 2007. Different letters indicate significant differences ($p < 0.05$) between sites.

	Sandy Bottom	Suffolk	Courtland East	Courtland West
Total Dissolved Phosphorus	9.82 (± 1.79) ^{bc}	73.22 (± 7.84) ^{a}	15.13 (± 2.14) ^{b}	40.01 (± 3.46) ^{c}
Dissolved Inorganic Phosphorus	4.55 (± 1.02) ^{a}	56.39 (± 5.43) ^{b}	13.51 (± 1.62) ^{a}	32.43 (± 2.52) ^{c}
Dissolved Organic Phosphorus	5.56 (± 0.82) ^{a}	16.84 (± 2.54) ^{b}	3.66 (± 0.66) ^{a}	8.65 (±12.40) ^{a}
Ammonium	50.30 (± 9.29) ^{a}	47.20 (± 5.43) ^{a}	85.81 (± 15.59) ^{ac}	123.11 (± 14.78) ^{c}

Porewater Depth Profiles

Porewater depth profiles (Figures 34-37) showed the same trends in seasonal changes as the previous plots of the porewater mean over top 20 cm. There was considerable variation with depth; however, there were no consistent trends that could be observed with increased depth for any of the parameters.

Figure 34. Depth profiles of mean (± 1SE) porewater total dissolved phosphorus (µM) in *Typha* and non-*Typha* stands, at all study sites, summer 2007.

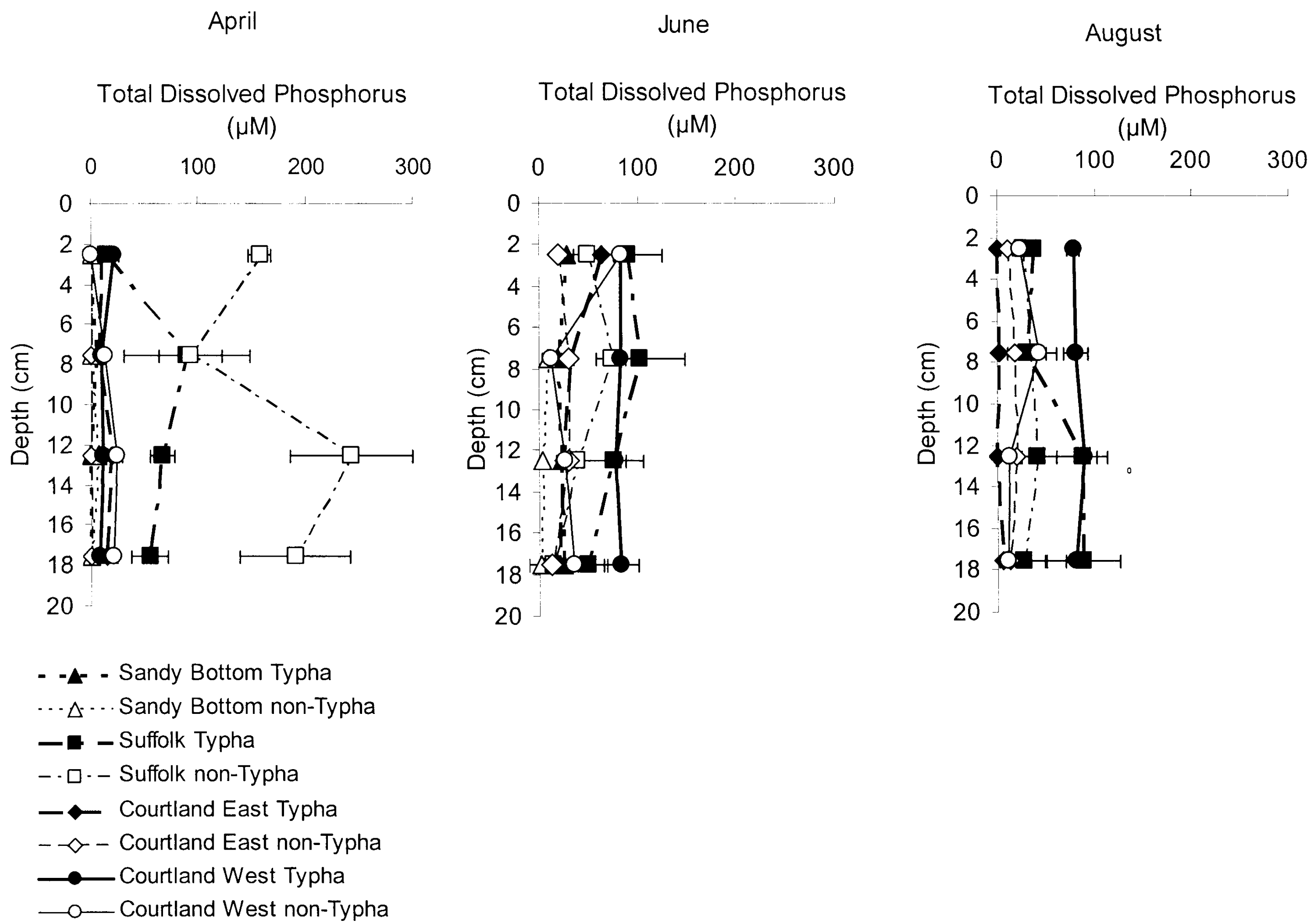


Figure 35. Depth profiles of mean (± 1SE) porewater dissolved inorganic phosphorus (µM) in *Typha* and non-*Typha* stands, at all study sites, summer 2007.

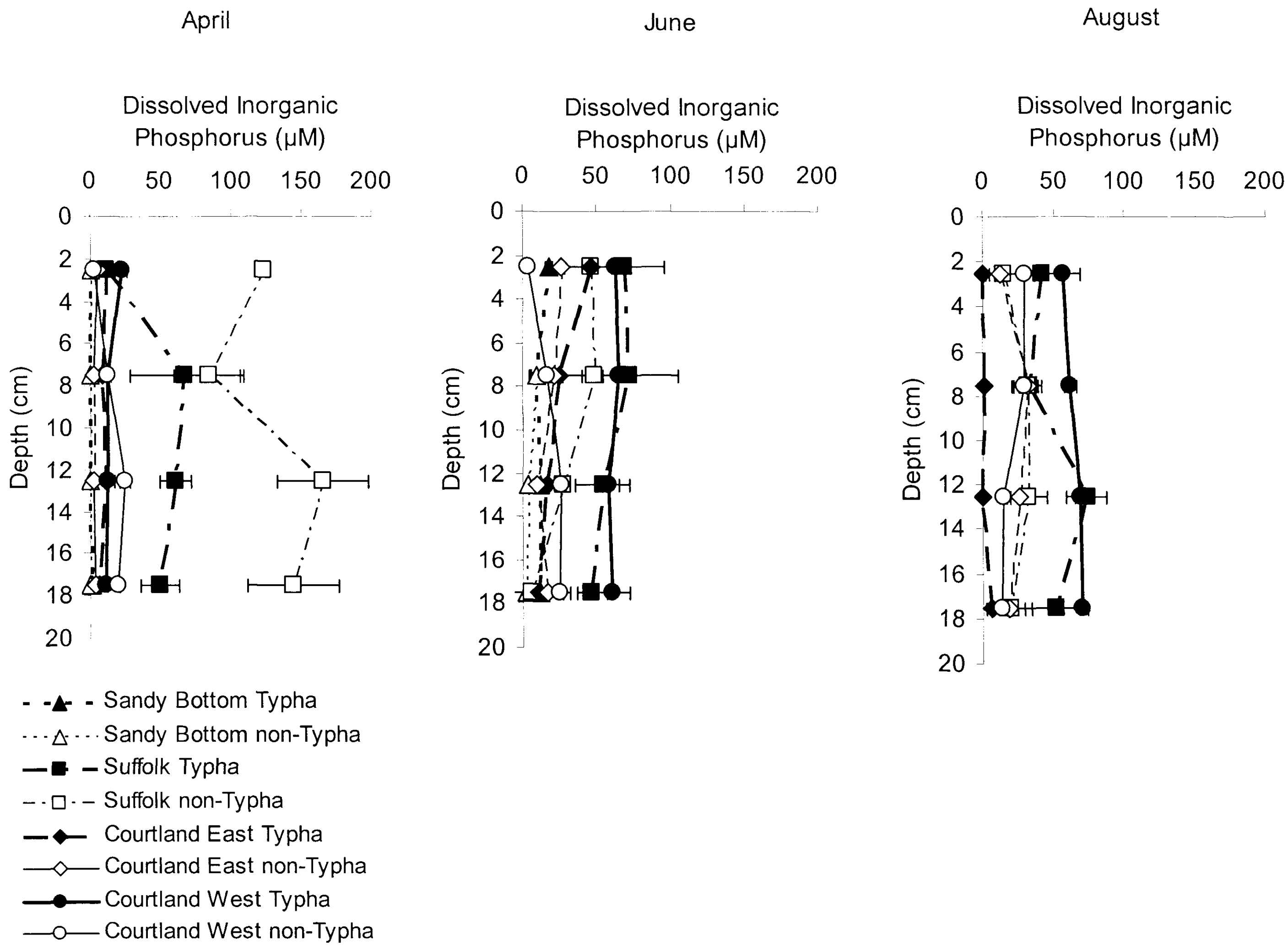


Figure 36. Mean (± 1SE) porewater dissolved organic phosphorus ratio (μM) in *Typha* and non-*Typha* stands, at all study sites, summer 2007.

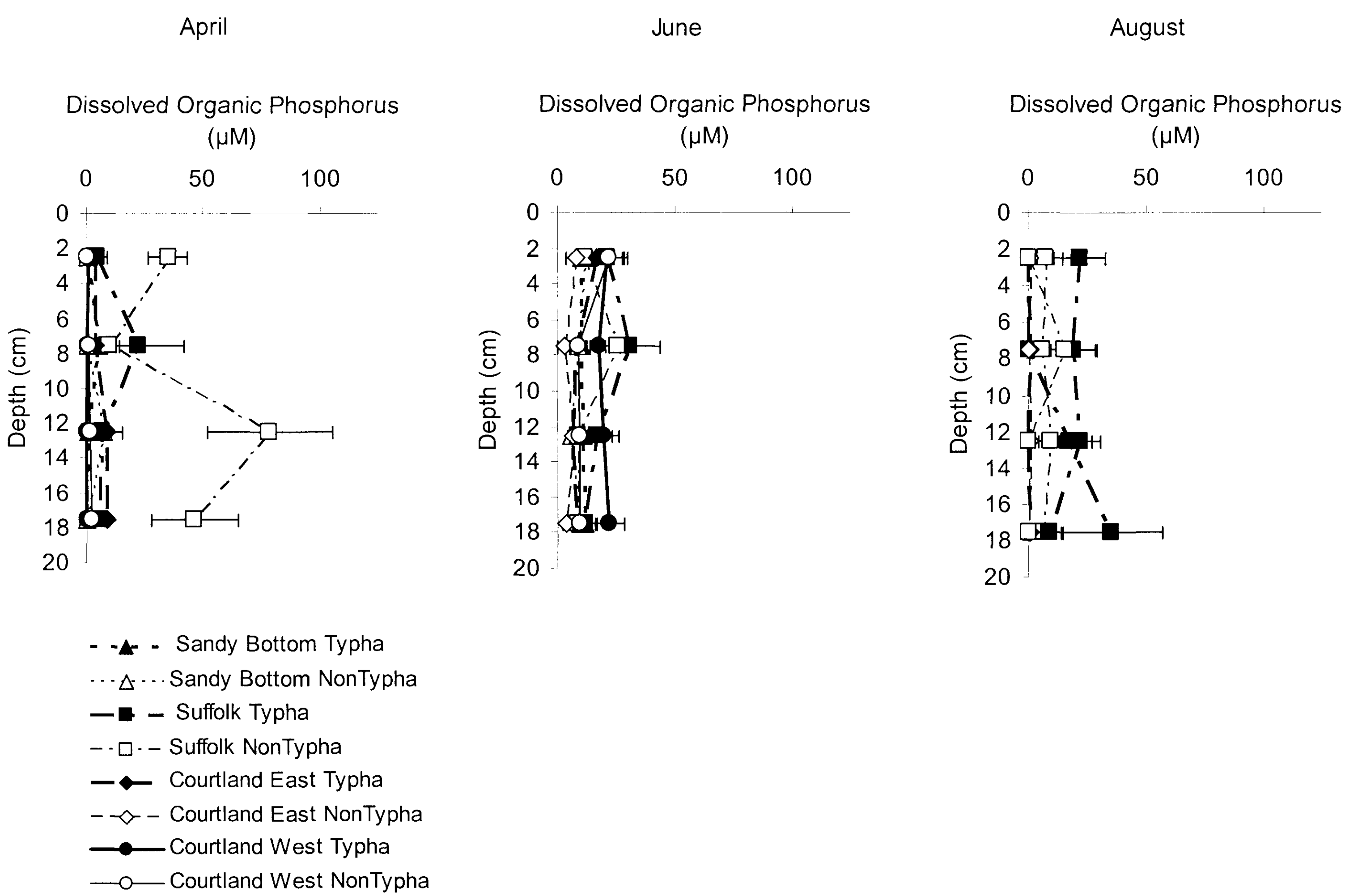
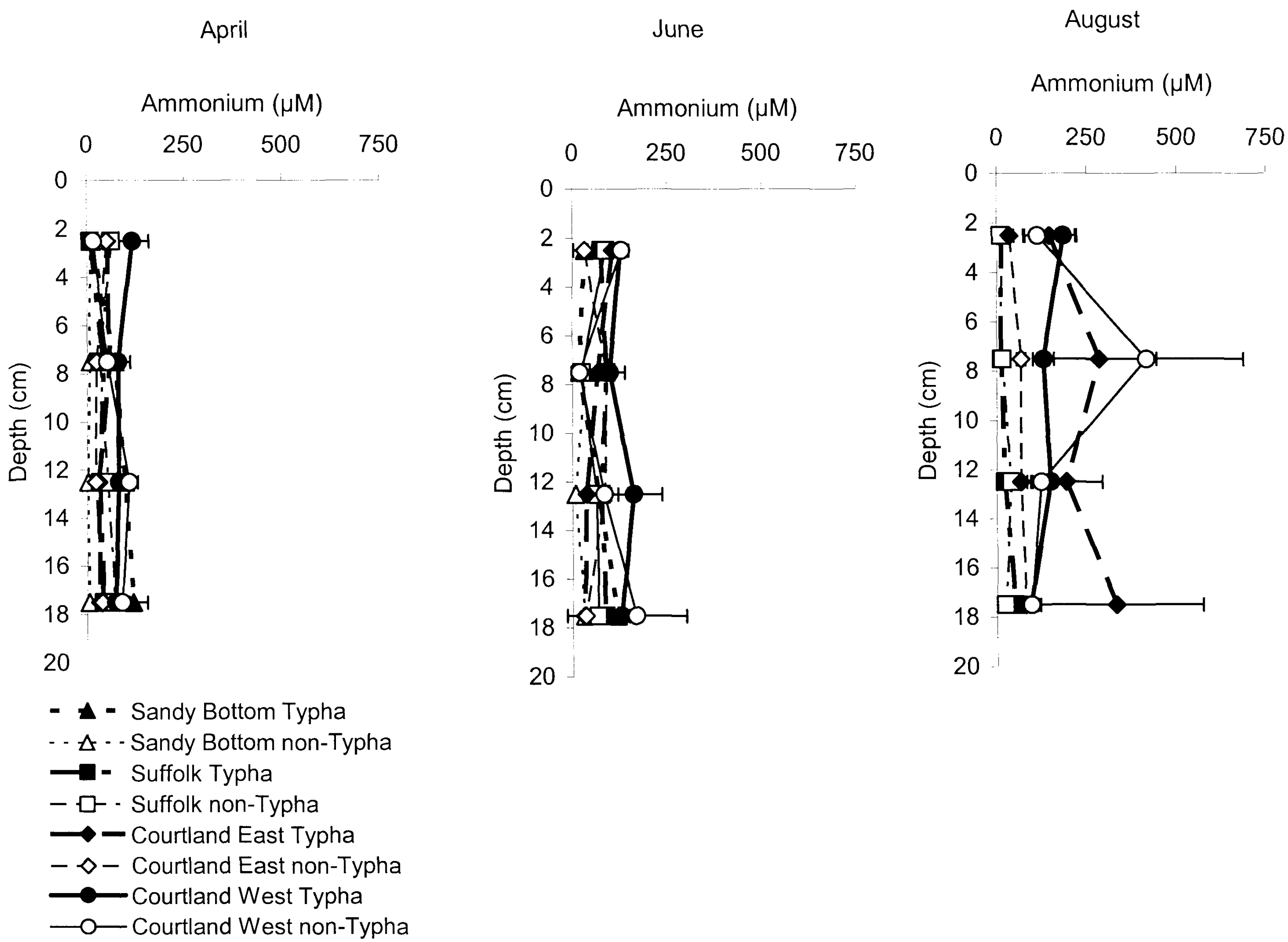


Figure 37. Depth profiles of mean (± 1SE) porewater ammonium (µM) in *Typha* and non-*Typha* stands, at all study sites, summer 2007.



Typha Total Nitrogen

In 2006, the *Typha* leaf TN at CE was significantly lower than SB and CW, possibly due to a dip in TN that occurred in August and September (Figure 38). In 2007, no significant differences in *Typha* leaf TN were observed between sites. In 2007 the early season sampling, April and May revealed higher TN and TP concentrations in new leaves. By June the TN and TP levels in the leaves had returned to levels similar to what was seen in 2006 (Figures 38 and 40). This higher TN and TP concentration early in the season resulted in slightly higher mean TN and TP in 2007.

Figure 38. Mean (± 1 SE) of *Typha* leaf total nitrogen, at all study sites, summer 2006.

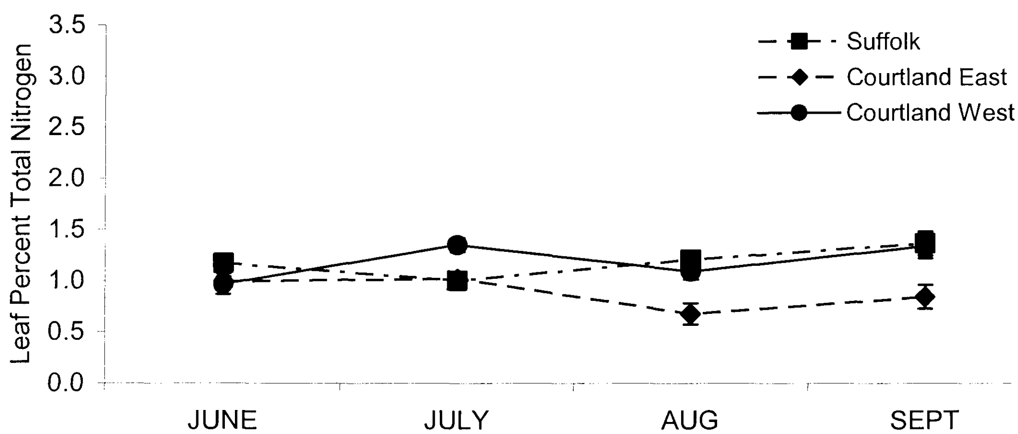
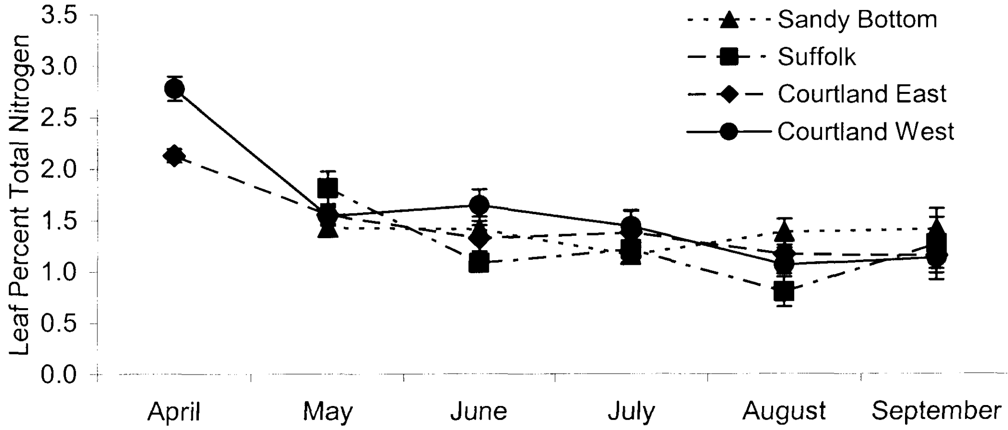


Figure 39. Mean (± 1 SE) of *Typha* leaf total nitrogen, at all study sites, summer 2007.



Typha Total Phosphorus

In 2006, SF had significantly higher leaf TP than CE or CW (Table 16). In 2007, the only significant difference in TP between sites was between CW and SB (Table 17).

Figure 40. Mean (± 1 SE) of *Typha* leaf total phosphorus, at all study sites, summer 2006.

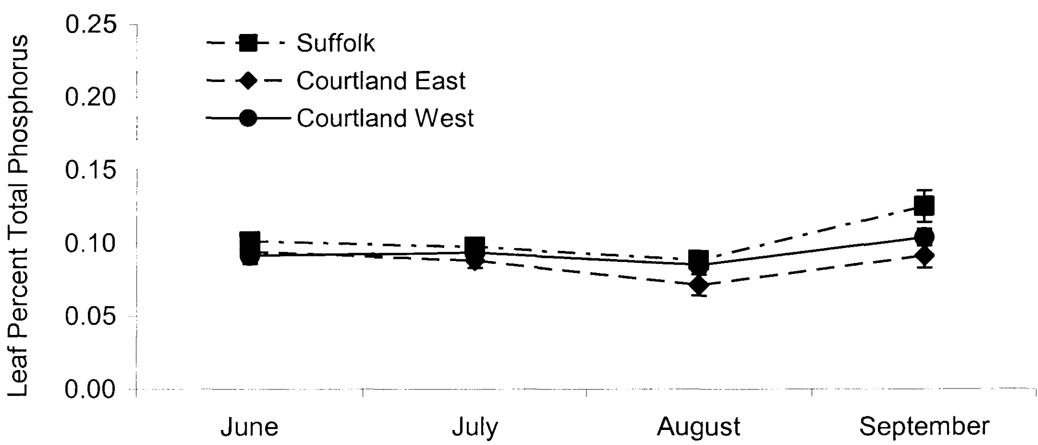
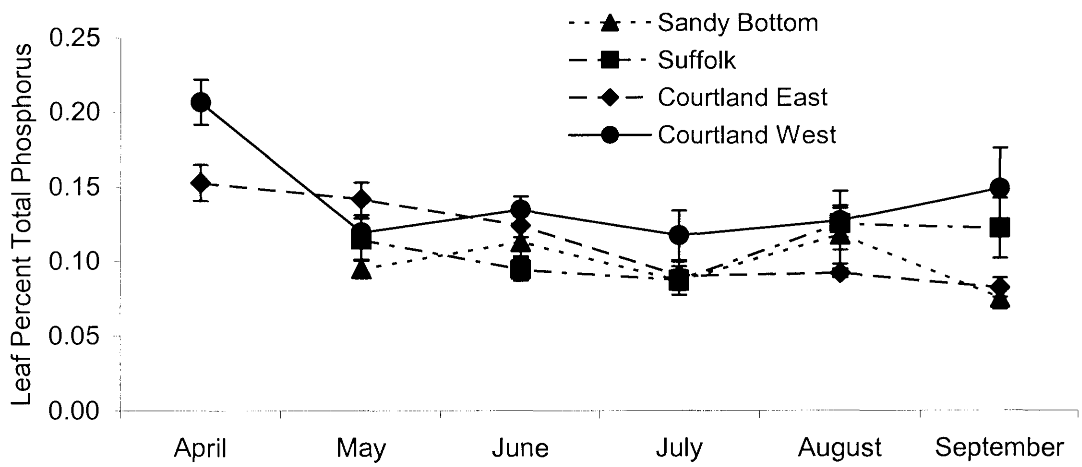


Figure 41. Plots of mean (± 1 SE) of *Typha* leaf total phosphorus, at all study sites, summer 2007.



<u>*Typha* Nitrogen to Phosphorus Ratio</u>

In 2006, no significant differences were seen in *Typha* leaf N:P ratio between any of the sites (Figure 42), the range of *Typha* leaf molar N:P ratio was 23-28. In 2007, the range of molar N:P ratio at all sites was 26 to 34.

Figure 42. Mean (± 1 SE) of *Typha* leaf nitrogen to phosphorus ratio (N:P), at all study sites, summer 2006.

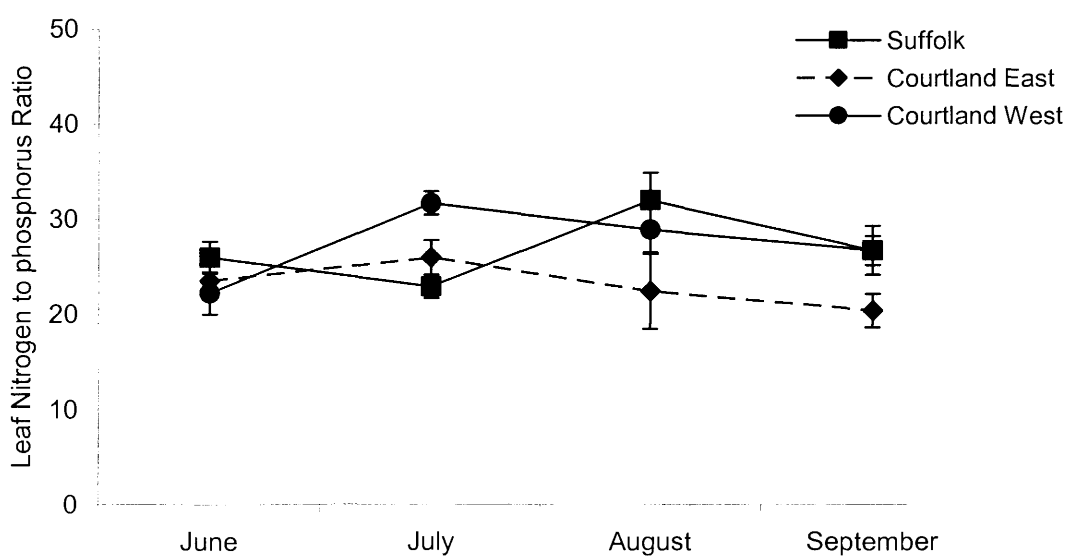


Figure 43. Mean (± 1 SE) of *Typha* leaf nitrogen to phosphorus ratio (N:P), at all study sites, summer 2007

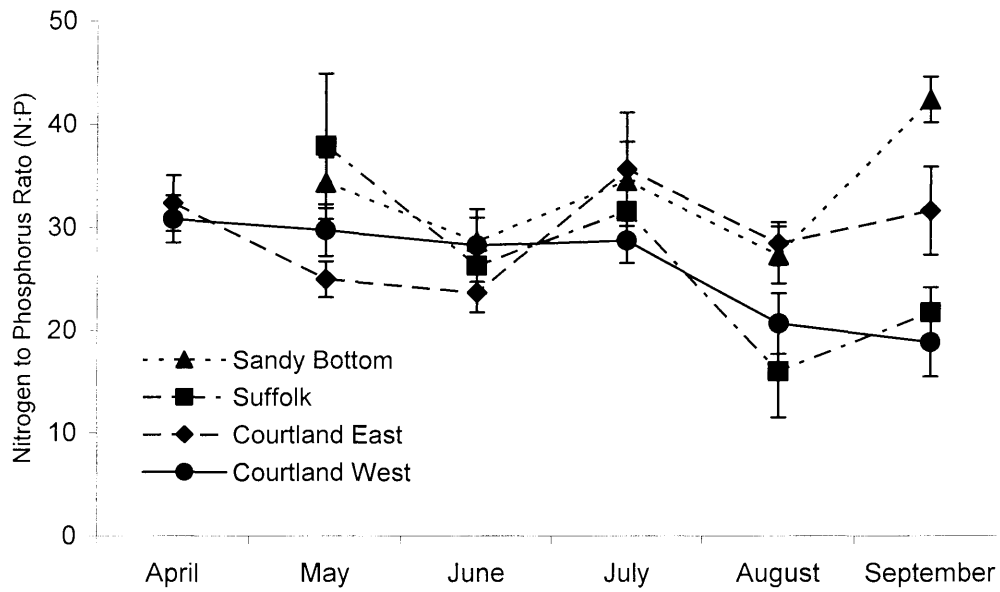


Figure 44. Monthly *Typha* leaf nitrogen versus phosphorus concentrations, at all study sites, summer 2006 and 2007, lines indicate where critical N:P ratios that indicate N and P limitation are located (N:P < 31 indicates N limitation, and N:P > 35.5 indicates P limitation)(Koerselman and Meuleman 1996)

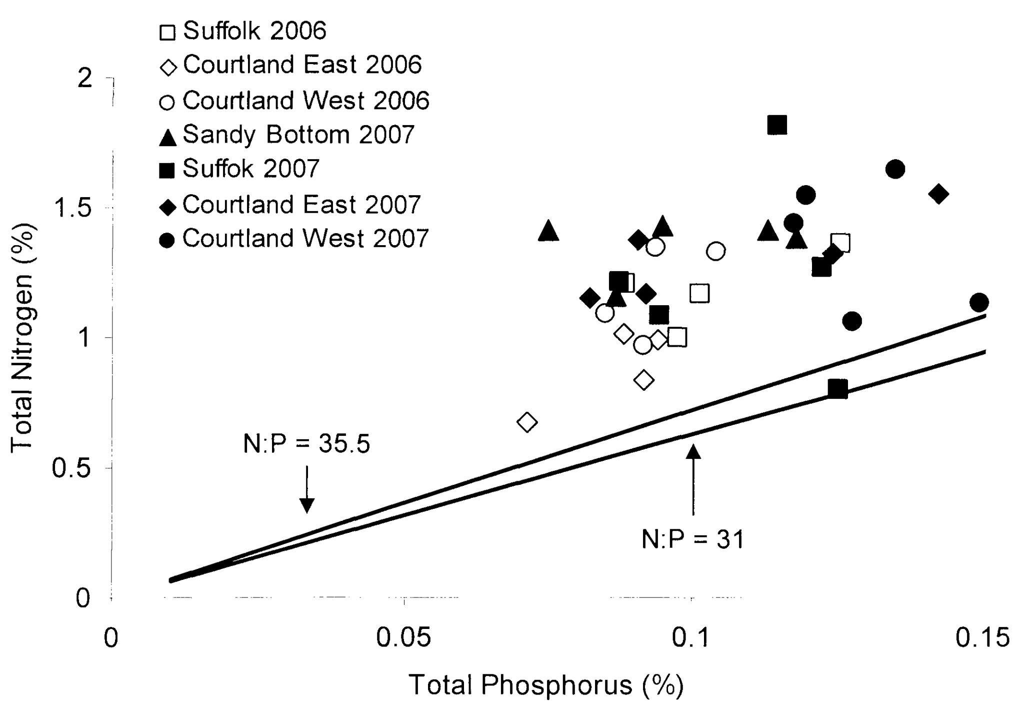


Table 16. Summary of mean *Typha* leaf nutrients (± 1 SE) for each site, summer 2006. Different letters indicate significant differences ($p < 0.05$) between sites.

2006	Suffolk	Courtland East	Courtland West
Total Nitrogen (% total dry weight)	1.20 (± 0.39) [a]	0.88 (± 0.46) [b]	1.15 (± 0.047) [a]
Total Phosphorus (% total dry weight)	0.102 (± 4.0 E^{-3}) [a]	0.086 (± 3.5 E^{-3}) [cb]	0.093 (± 2.5 E^{-3}) [c]
Nitrogen to Phosphorus Ratio	26.8 (± 1.11) [a]	23.2 (± 1.27) [a]	27.6 (±1.1) [a]

Table 17. Summary of mean *Typha* leaf nutrients (± 1 SE) for each site, summer 2007. Different letters indicate significant differences ($p < 0.05$) between sites.

2007	Sandy Bottom	Suffolk	Courtland East	Courtland West
Total Nitrogen	1.32 (± 0.042) ^{a}	1.21 (± 0.095) ^{a}	1.47 (± 0.071) ^{a}	1.66 (± 0.10) ^{a}
Total Phosphorus	0.095 (5.0 E $^{-3}$) ^{a}	0.11 (5.8 E $^{-3}$) ^{ab}	0.117 (5.4 E $^{-3}$) ^{ab}	0.143 (7.7 E $^{-3}$) ^{b}
Nitrogen to Phosphorus Ratio	33.65 (± 1.71) ^{a}	26.47 (± 2.22) ^{b}	29.09 (± 1.36) ^{ab}	26.09 (±1.27) ^{b}

Table 18. *Typha* leaf carbon to nitrogen to phosphorus ratio (C:N:P), at all study sites, summer 2006 and 2007.

	2006	2007
Sandy Bottom	Not sampled	1127:31:1
Suffolk	1128:25:1	997:25:1
Courtland East	1351:317:1	974:28:1
Courtland West	1238:393:1	756:25:1

Table 19. Summary of mean soil, porewater, and plant N:P ratios, just Typha stands, for each site, summer 2007.

	Sandy Bottom	Suffolk	Courtland East	Courtland West
Bulk Soils (TN:TP)	21.5 ± 2.8	25.3 ± 3.83	60.4 ± 16.6	47.4 ± 7.5
Porewater (DIN:DIP)	117.8 ±39.9	0.88 ±0.11	92.0 ±44.5	3.41 ±0.37
Porewater (DIN:DIP) Typh Tissue (TN:TP)	33.7 ±1.71	26.5 ± 2.2	29.1 ± 1.36	27.0 ± 1.27

SOIL, POREWATER, AND PLANT RESULTS SUMMARY

Principal Components Analysis

Principal components analysis (PCA) (Minitab 15) of the bi-monthly means (April, June, and August) of soil and porewater parameters in T and NT stands at all sites revealed that the first component, that accounts for 50% of the variation between sites, is primarily controlled by nutrient availability. Soil TC, TN, TP, and porewater TDP and DIP are found at one end of the first component and porewater NH_4^+ is at the other end (Figure 45). The monthly means for SF T and NT (Figure 45 in oval), are all at the upper end of the first component, this is consistent with the significantly higher nutrient concentrations seen at SF. Porewater TDP and DIP are at opposite ends of the first component from porewater NH_4^+ availability, indicating that in sites where porewater P is high, the N availability is low.

Figure 46 shows the PCA comparison of bimonthly means of just T stands and includes the variables *Typha* ramet density and *Typha* leaf N:P ratio, as well as the soil and porewater parameters. The first component is controlled primarily by nutrient availability. *Typha* leaf N:P ratio seems to vary with porewater NH_4^+ concentration. This indicates that the sites with higher ammonium availability also have higher leaf N:P ratios, and is consistent with use of leaf N:P as a general measure of nutrient limitation.

Figure 45. Plot of results of principal components analysis of soil and porewater parameters for *Typha* and non-*Typha* stands, at all study sites, summer 2007.

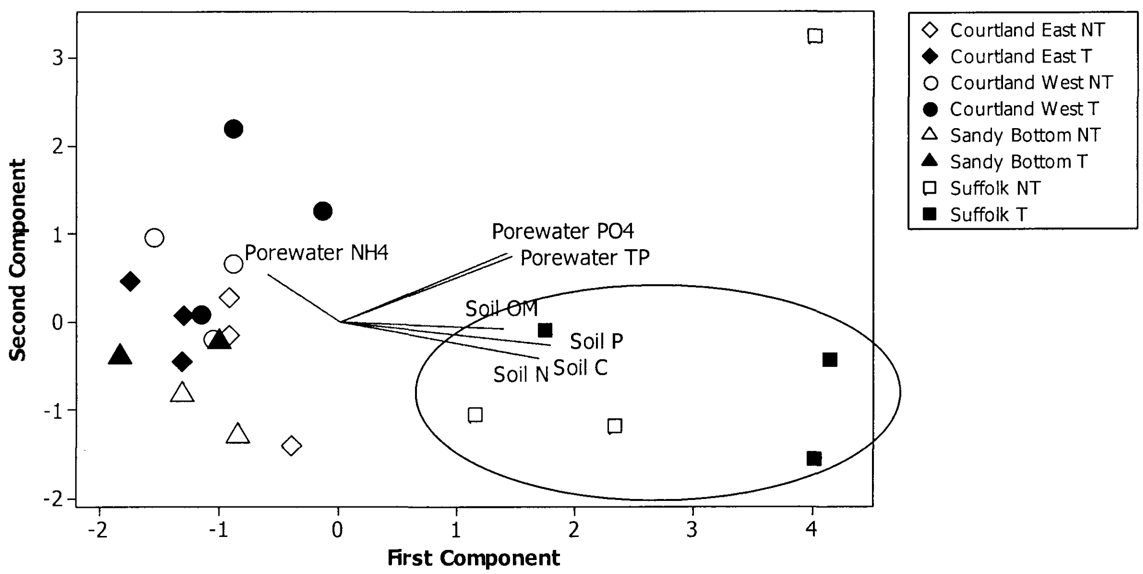
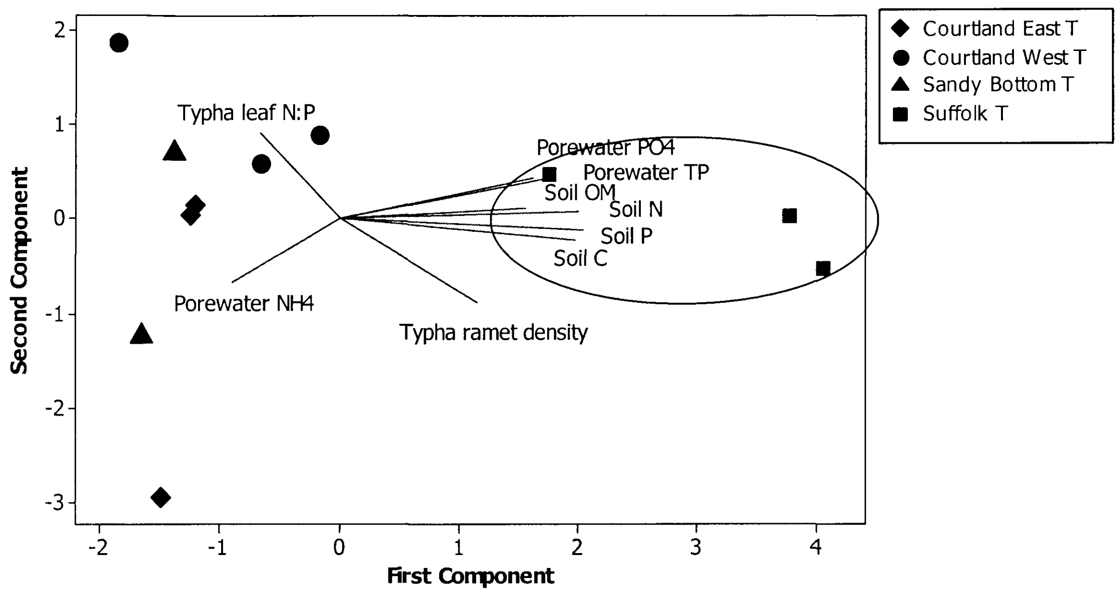


Figure 46. Plot of results of principal components analysis of soil and porewater parameters, *Typha* leaf N:P, and *Typha* ramet density for *Typha* stands, at all study sites, summer 2007.



Nutrient Uptake Experiment Results

Nutrient Uptake Experiment

No depletion was observed in phosphate (PO_4^{3-}) in any of the treatments (Figure 47). There seems to be a slight depletion of ammonium (NH_4^+) (Figure 48) however, a two-tailed t-test comparing the initial and final NH_4^+ concentrations showed no significant difference, therefore no conclusive statements can be made regarding NH_4^+ uptake by *Typha*.

Figure 47. Mean (± 1 SE) phosphate concentrations over time in uptake experiment all treatments

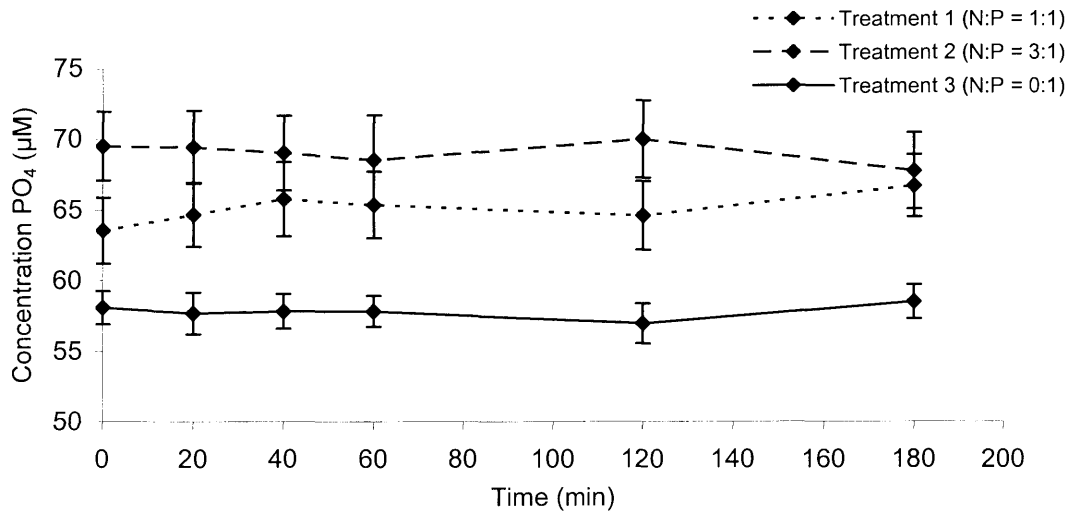
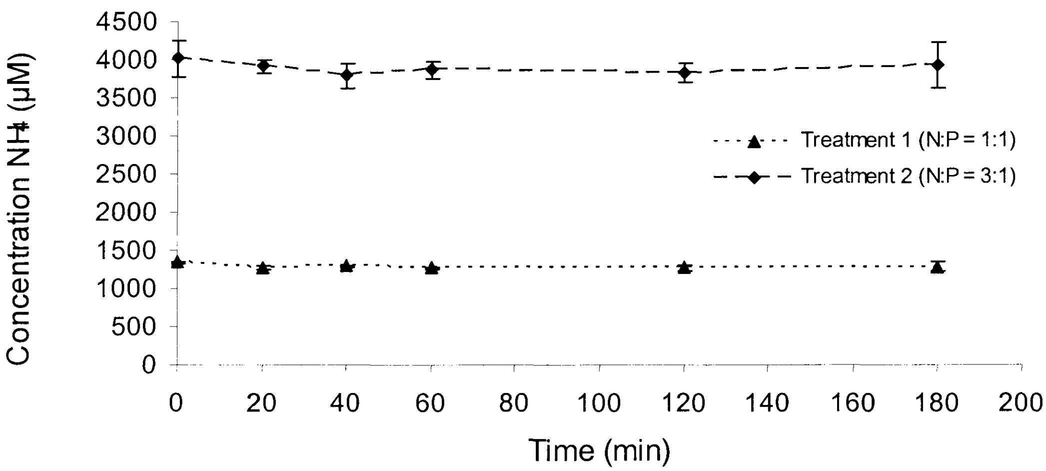


Figure 48. Mean (± 1 SE) ammonium concentrations over time in uptake experiment treatment 1 (1:1 N:P) and treatment 2 (3:1 N:P)



Discussion

Differences Between *Typha* and Non-*Typha* Stands

I hypothesized that there would be differences in soil and porewater parameters between *Typha* (T) and non-*Typha* (NT) stands within the study sites, and that these differences would help to explain the different vegetation communities. This was based on previous studies of *Typha* population expansion in response to phosphorus (P) enrichment (Craft et al. 1995, Craft and Richardson 1997). However, for most soil parameters, there were no significant differences or trends between T and NT stands. Soil percent organic matter (OM) showed no difference between T and NT at any sites, but the percent total carbon (TC) in soil was significantly higher at in NT at CW in 2006, and SF and CE in 2007. Because these sites were sampled in both years, but only exhibited significant differences in one year, these are not considered strong trends and more intensive sampling over a longer period of time is necessary to determine if these results indicate a trend in differences between T and NT stands. Similarly inconsistent results were observed for total nitrogen (TN), which in 2006 was higher in T stands at CW, and higher in NT stands at CE, with no difference observed at SF. In 2007, the difference at CW was again significant but reversed, with the NT stand having higher TN. No significance difference was seen in SF, SB, or CE in 2007. All the forms of P that were quantified (total phosphorus (TP), acid extractable phosphorus (AEP), and organic phosphorus (OrgP)) exhibited no significant difference between T and NT in any sites in 2006. In 2007, only TP was significantly higher in the NT stand at CW, and AEP was higher in the NT stand at CE. While these are both the older, more mature created sites, the lack of a consistent trend from 2006 to 2007, and only one form of P being different in each, does not allow interpretation of differences based on site age or *Typha* or non-*Typha* dominated vegetation assemblage.

Porewater sampling via diffusion samplers was conducted because it allows sampling of the soil solution in the matrix pores, which are the areas where roots come into contact with porewater (Harvey et al. 1995, Winger et al. 1998). The soil porewater serves as an intermediate pool of nutrients between the soil and plants and is the source from which plants are able to take up inorganic forms of N and P. As was the case with soil nutrients, there were no consistent significant differences in porewater nutrient concentration between T and NT stands for any of the sites. This further confirms the conclusion that the soil and porewater nutrient availability was not different in areas of these sites that were dominated by *Typha* and areas that were not. Therefore, it can be concluded that the soil and porewater parameters investigated in this study were not a major control on the presence or density of *Typha* in created wetlands less than 15 years old, and the differences in dominant vegetation type in these areas were due to other factors, such as propagule dispersal and inter-specific competition.

Differences Between Sites

Due to the lack of distinction between soil and porewater characteristics in T and NT stands, the T and NT stands within each site were combined for all inter-site comparisons. The initial experimental design assumed a grouping of the sites by age. However, large nutrient availability differences observed between the two younger sites, SB and SF, have made grouping these sites impractical. SB had very different hydrology and soil characteristics than SF, primarily due to epiaquic conditions that are a result of soil compaction that occurred during the wetland construction process. The impermeable clay pan in the soil profile has lead to perching of surface water and has prevented discharge of groundwater, resulting in extremely dry conditions during much of the summer (Daniels et al. 2005, Fajardo 2006). The very low OM measured at SB, a site that according to construction plans and permit requirements had 4% OM topsoil disked into the soil to a depth of 20 cm (Daniels et al. 2005, Fajardo 2006), indicates that either this OM addition did not occur to the level required by the permitting, or that it was very rapidly remineralized and lost from the system, due to the very dry soil conditions. Either way, the lack of OM in these soils has resulted in a fundamental difference between SB and SF. This difference is compounded by the fact that SF had very high OM additions to the topsoil during construction, in the form of partially composted leaf litter. This resulted in initial percent soil OM between 2 and 5% in the surface layers (pers. comm. W. L. Daniels). The OM additions at SF have lead to the extreme differences observed between SF and the other three sites in all soil parameters.

Generally, SB was more similar to the older sites (CE and CW) than to SF. This can be seen in the arrangement of SB and SF at opposite ends of the first principal component axis, which represents soil and porewater nutrient concentrations and soil OM (Figures 45 and 46). Therefore, much of the discussion of soil characteristics in older and newer created wetlands will focus on differences between SF and the older sites (CE and CW).

The results of the vegetation community analyses (Chapter 3) indicated that there were no trends in differences between the individual sites in species richness and Shannon diversity indices. This was not the case for the nutrient results, as there was a definite trend of significantly higher nutrient availability and OM in SF. This site had consistently higher OM, TC, and TN than all other sites in 2006 and 2007. The older sites did not receive the same type of OM amendments and despite over 15 years of OM accumulation have not reached the same level of soil OM as SF. Because of the very low level of OM at the older sites, the increase in OM of 1% of bulk soil content that was measured at SF, CE, and CW (Table 13) is most likely not representative of the normal annual increase. Long-term sampling is needed to understand the incorporation of OM in created wetlands over long periods of time. The inability of created wetlands to accumulate OM to a level equivalent to natural wetlands has been identified by other researchers and has led to the practice of higher levels of OM incorporation during wetland construction (Stolt et al. 2000, Daniels et al. 2005). This is the cause of the change in construction techniques between the construction of CE/CW and SF, though these protocols do not appear to have been followed at SB.

SF also had much higher porewater concentration of total dissolved phosphorus (TDP), dissolved inorganic phosphorus (DIP), and dissolved organic phosphorus (DOP), than the other sites, this is primarily due to very high concentration of all forms of P measured at SF in April, which then dropped off and were similar to the concentrations measured at CE and CW. SB had a consistently lower porewater concentration of all forms of P compared to the other sites (Figures 30-32, Table 15). The opposite trend is seen in porewater ammonium ($NH4^+$), with CE and CW having higher concentrations than both SF and SB (Figure 33, Table 15).

Changes in Soil Nutrient Concentration From 2006 to 2007

The relationship between soil TC and TN at all sites showed a very strong correlation ($r^2 = 0.82$) (Figure 19) as would be expected since the primary form of N in these soils was organic. The magnitudes of TC and TN were larger at SF; however, the ratios were similar between the sites. There was no change in the relationship between TC and TN from 2006 to 2007. The relationship between TC and TP at these sites was much more variable, this is also as one would expect since the amount of TP is not purely dependent on organic forms of P, but also includes inorganic P that is sorbed and complexed with soil minerals and clay. Another aspect of the variability in the C:P is the large shift in TP. In 2007, all the sites had less TP and similar or higher TC, as indicated by the much steeper regression slope (Figure 22). A similar shift in the regression slope can be seen in the ratio of TN to TP from 2006 to 2007 (Figure 29).

The extremely large change in soil TP between 2006 and 2007 can most likely be partially explained by ecological factors, such as regional climate and vegetation sequestration; however, it seems unlikely that this extremely large amount of soil TP could be removed form the system by natural factors alone within one year. Therefore, it may indicate that there was an inconsistency in either sample collection or analysis between 2006 and 2007. While I have reviewed all the protocols and am fairly confident that I did not do anything different between the two years, I have to admit that there may have been some small change that resulted in very different values in the two years. It must also be said that the changes observed may be a result of a combination of natural factors as well as sampling error, and there is no way to tease out the degree of influence of each factor from this dataset.

A summary of the changes in soil nutrients between 2006 and 2007 (Table 13) indicates that the increases and decreases that are occurring are consistent across all three sites for OM, TC, and TN. The decrease in TP is half as much at the older sites as at SF. From 2006, the TN in all sites increased and the TP decreased, resulting in much higher soil N:P ratios in all sites. The N:P ratio at the older sites increased ten times at CE and CW, compared to three times at SF. This seems to indicate that the rate of P loss and N addition at the older sites may be increasing. However, in order to determine if this is a valid successional trend caused by environmental factors, and not an artifact of sampling error, the soil nutrient levels in a large number of sites would need to be monitored for a number of years.

The study sites do not have surface connection to other bodies of water, which limits the loss of particulate organic phosphorus (POP) to outflow, and makes plant uptake and sequestration in perennial biomass the primary removal pathway of soil P. No increase in TP was measured in *Typha* aboveground tissue from 2006 to 2007; however, there may be storage of P in belowground *Typha* tissue or biomass of other dominant perennials that are found at the sites. Because the decrease in soil P occurs across the entire site, it is likely that the large perennial species that are dominant or co-dominant across these sites, such as *J. effusus* and *S. cyperinus,* are also playing a part in sequestration of P in perennial vegetative growth.

Greenhouse Uptake Experiment

It was initially hypothesized that *Typha* would take up phosphate (PO_4^{3-}) at a constant rate, under a variety of ammonium (NH_4^+) concentrations, and that if *Typha* plants were able to incorporate PO_4^{3-} at a high rate, irrespective of the amount of available N, it would suggest it has the ability to take advantage of pulses in P availability. However, this was not observed, no uptake of PO_4^{3-} or NH_4^+ was observed in any of the treatments. The lack of apparent utilization of NH_4^+ and PO_4^{3-} from outside sources may be caused by the preferential use of nutrients stored in rhizomes for aboveground growth regardless of outside nutrient availabilities. This large supply of nutrients stored in rhizomes may allow *Typha* to maintain growth and expansion as nutrient supplies, particularly P, decrease in the surrounding soil. The evidence that *Typha* has large rhizomatous nutrient stores further supports the hypothesis that soil P can be removed and stored in *Typha* belowground biomass.

Typha Leaf Tissue

While nutrient limitation is considered an important control on the vegetation community, it is very difficult and time-consuming to measure via experimental fertilization (Chambers and Fourqurean 1991, Koerselman and Meuleman 1996, Bedford et al. 1999). Therefore, many metrics have been investigated to estimate nutrient limitation more easily and with fewer disturbances to the ecosystem. One technique evaluated by Koerselman and Meuleman (1996) involves the use of the molar N:P ratio in live aboveground tissue. They tested this approach by assessing 40 wetland systems in northern Europe for which nutrient limitation had been determined experimentally, and determined that the live tissue N:P effectively estimated the nutrient limitation in all but one of the systems. In their study they used N:P by mass, however their results are converted to molar N:P here, for ease in comparison to the results of this study. They concluded that N:P ratio < 31 indicates N limitation, N:P ratio > 35.5 indicates P limitation, and N:P ratio between 31 and 35.5 indicates that both nutrients are limiting. Koerselman and Meuleman were satisfied with how well the critical values they identified, predicted nutrient limitation. However, Chambers and Fourqurean (1991) evaluated the effectiveness of metrics that used the molar N:P ratio in soil, porewater, and leaf tissue to measure nutrient limitation in *Peltandra virginica* in a tidal freshwater wetland in southeastern VA, and concluded that these metrics often gave conflicting results. I also found conflicting predictions based on the N:P ratios in the soil and plant tissue. Based on Koerselman and Meuleman's critical values, all the sites used in this study were N limited in both years (Figure 44), however when comparing the plant tissue molar N:P ratio to the soil N:P ratio in the same site, a more complicated picture of changing nutrient limitation over time emerged.

There were no significant differences in *Typha* aboveground tissue N:P ratio in any of the study sites. The N:P ratio ranged from 20 to 30 in 2006 and from 15 to 35 in 2007. This wide range of variation was observed within all sites (Figures 42 and 43) and seems to indicate that even for a single population, growing under similar conditions, the range of tissue molar N:P ratios can be very large. In 2006 and 2007, the majority of the sampling points were at or below the critical molar N:P ratio of 31, indicating N limitation according to Koerselman and Meuleman (1996). However, the month-to-month variation within a single site was often larger than 4.5, the range between the critical values for N and P limitation (Koerselman and Meuleman 1996). This seems to indicate that the range they identified may be too fine to account for all the variation that can occur within a population, and presumably between populations.

A study conducted by McJannet et al. (1995) measured a molar N:P ratio of 9.25, in *Typha* x *glauca* grown under nutrient enrichment, these results were much lower than the range I measured, and according to Koerselman and Meuleman (1996) indicated that these plants were also N limited. However, since N and P were both available in high quantities, in their experiment the excess P in the plant tissue may represent luxury uptake of P relative to N, which can occur during periods of very high P availability (McJannett et al. 1995). The lack of N or P uptake that was observed in *Typha* plants propagated from rhizomes in sterile sand mixtures, supports the conclusion that *Typha* have large stores of nutrients in belowground tissue, possibly from luxury uptake, that is utilized for growth under low nutrient conditions. Under very high nutrient enrichment, luxury uptake may also be expressed in aboveground tissue, as was the case in the study by McJannet et al. (1995). However, I did not observe leaf tissue N:P ratios less than 10, indicating that P is not available in high enough levels to elicit luxury uptake and storage in aboveground tissue.

Since the focus of this research was to determine if environmental factors had an effect on *Typha* dominance, it was the only species for which leaf tissue was analyzed. Therefore inferences about relationships between *Typha* N:P ratio and soil N:P ratio are only made for the T stands in the sites. However, since the soil characteristics were not significantly different in T and NT stands it is likely that the same soil processes were taking place across the entire sites, regardless of dominant vegetation species.

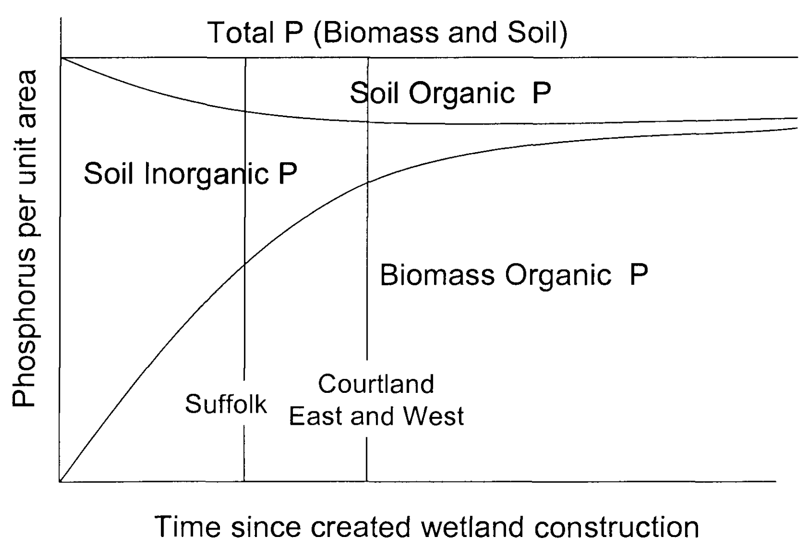
The plant tissue molar N:P ratio ranges between 25 to 35 in all sites, since all sites had areas of *Typha* expansion, it can be assumed that these plants were not nutrient limited. Therefore, I assumed that 25-35 is an optimal range of N:P ratio in *Typha* tissue.

The soil range of N:P ratios in 2006 (5 to 7) was very low compared to the optimal *Typha* N:P, which would indicate that the sites were N limited, this is also indicated by comparison to Koerselman and Meuleman (1996) critical values. However, in 2007 the soil N:P ratios were higher in all sites. SF and SB had N:P ratios (21-26) that were very similar to what was consistently seen in *Typha* leaf tissue, indicating no limitation. In 2007, the range of CE and CW soil N:P ratios were much higher (47-60) than the *Typha* leaf levels, which would indicate P limitation. The wide range in soil N:P ratio results in all of these sites between 2006 and 2007, may indicate that changes in soil N:P ratios do not have an immediate effect on aboveground tissue nutrient concentrations in *Typha*. Whether these changes are evident in belowground tissue or other vegetation types is not known, as these were not sampled in this study. However, the decrease in soil TP over time that was observed in these sites seems to indicate that it is being lost from the system, primarily to sequestration in perennial plant tissue.

Increasing Phosphorus Limitation with Site Age

Vitousek and Walker (1987) proposed a model for P dynamics in volcanic soil primary succession, which may be useful in understanding P dynamics in created wetlands. In newly created volcanic soil, there is no OM and relatively high abundances of mineral P. This is very similar to initial soil conditions in created wetlands, where primary succession occurs on previously upland subsoils that are devoid of OM and have readily available inorganic P, in the form of metal oxyhydroxides and clay complexes. The adsorbed and complexed inorganic P is released following inundation and lowering of redox potentials. This initial high P availability is rapidly taken up and stored in perennial plant tissue, a portion of the plant OrgP is restored to the soil as detritus and is remineralized by bacteria, releasing inorganic P, which is then rapidly taken up by plant growth. As the live aboveground and belowground biomass increases, especially in sites dominated by large perennial species, this process of uptake and storage of P in plant biomass, results in a decrease in the amount of soil TP as the site ages. This can lead to a "terminal steady state" of phosphorus deficiency in which OrgP is the primary form of P in soil and very rapid uptake occurs upon remineralization (Walker and Syers, 1976). The proposed conceptual model of changes in forms of P over time can be seen in Figure 49. The approximate locations on the time continuum of SF and CE/CW can also be seen in Figure 49. These locations are based on the relative proportions of forms of soil P measured at these sites in 2007.

Figure 49. Conceptual model of proposed phosphorus dynamics in soil and plant biomass in created wetlands over time. Includes locations of Suffolk and Courtland East and West study sites on the trajectory of soil primary succession, based on soil phophorus measurements in 2007.



In the created wetlands used in this study, the primary sources of N were surface runoff, incorporation of detrital OM, and atmospheric deposition. The major sources of N loss are sequestration in perennial biomass and denitrification, since there was no outflow of surface water from these sites. It can be concluded that the rate of N addition was greater than the rate of N loss from these systems due to the observed increase in soil TN that was measured between 2006 and 2007. If this is a consistent trend, it may indicate an increase in N availability in created wetlands as they age, this would hasten the increase in soil N:P ratio as the site ages.

Typha may be able to capitalize on the high availability of P relative to N early in the site development, and expand rapidly, and then as P abundance decreases relative to N, *Typha* may be able to maintain itself, because of stores in the rhizomes, but is not able to expand as readily. This is supported by the observation of rapid *Typha* expansion at SB, the site that had the lowest soil N:P in 2007. As created wetlands age the soil N:P increases, once it is greater than 35 (the highest N:P measured in *Typha* tissue) the *Typha* population may become P limited. Because of large stores of nutrients in rhizomes, *Typha* may be able to continue to expand under this P limitation, but eventually this terminal steady state of P deficiency (Walker and Syers 1976) will results in less expansion and dominance of the vegetation community by *Typha*. This is supported by anecdotal reports of decreases in *Typha* density and stand area in older created wetlands (pers. comm. Steve Russell and Leo Snead; Virginia Department of Transportation, Richmond, Virginia USA (VDOT)). More research is needed to test this hypothesis, and it would most likely require repeated annual sampling of soil nutrients and *Typha* stand area and density. Hopefully, the results of this research can be used as a starting point to continue to measure soil nutrient availability and *Typha* stand density in created wetlands, in order to better understand the successional dynamics of nutrient availability in these systems.

Chapter 5: Conclusions and Recommendations

Conclusions

No Negative Effect Associated with *Typha* Dominance

Analysis of the vegetation communities in *Typha* (T) and non-*Typha* (NT) dominated stands reveal that *Typha* dominance did not consistently lower species richness (SR) or Shannon diversity in any of the wetlands studied, in fact in some cases SR and diversity were higher in the T stands. These findings are particularly important because of the current management practices that use cutting and herbicide spraying to remove standing *Typha* vegetation from created wetlands. This practice is mainly based on vegetation community changes that have occurred following *Typha* invasion in other disturbed wetlands, often in response to nutrient enrichment (pers. comm. S. Russell and L. Snead; VDOT). To my knowledge, before this project was undertaken, no research had been done in southeastern VA created mitigation wetlands to investigate the basis for *Typha* removal. Since I was able to document that the presence of *Typha* did not negatively affect the plant communities in the created wetland sites, it appears that the removal of *Typha* may not be necessary. The rational for removal, based on the assertion that *Typha* dominance limits biodiversity, was not supported by my data. Therefore, other approaches need to be investigated to increase vegetation community diversity in created wetlands, such as repeated plantings or seeding with native annual and perennial plants during the first few years of site development.

No Difference in Nutrient Concentration Between *Typha* Stands and Non-*Typha* Stands

No consistent differences in soil nutrient availabilities were found between T and NT stands in any of the sites, this seems to indicate that within a single site the different vegetation guilds were not controlled by nutrient availability, and that other factors such as propagule dispersal, microtopography, and interspecific competition may have been controlling the community composition. The nutrient concentration across the site varied in a similar way over time within each site and at all study sites, this suggests that successional soil development processes were more important than within site variability in determining soil nutrient content.

There were also no consistent differences in porewater nutrients between T and NT stands. Porewater serves as an intermediary between nutrients held in soil (inorganic and organic) and nutrients held in plant biomass (organic); it is constantly receiving nutrient inputs from bacterial remineralization of organic matter, and these nutrients are then removed via uptake by vegetation. Porewater nutrient concentration represents a very dynamic nutrient pool. Therefore, it was very difficult to make conclusions about the nature of nutrient availability and limitation based on the porewater measurements taken in this study.

Changes in Soil Nutrient Availability as Created Wetlands Age

The changes in soil N and P availabilities that were measured between 2006 and 2007 may fit a trend of decreasing soil P and increasing soil N, as the sites age. This cannot be validated from this data. However, it is an interesting hypothesis about the trajectory of soil nutrient dynamics in created wetlands, and needs to be studied in more detail. The loss of TP from the soil is primarily caused by the uptake and sequestration of P in perennial plant biomass. It is likely that this is a function of the entire vegetation community, not just *Typha*. It is possible that *Typha* are able to capitalize on the higher availability of P that occurs early in the site development and expand rapidly, then as P abundance decreases relative to N, the population is able to maintain itself by using nutrient stores in the rhizomes, but is not able to expand as readily. This would presumably create a situation in which the vegetation community is less dominated by *Typha* and lead to a more species rich community as created wetlands mature. If this hypothesis is correct, it would suggest that the vegetation community itself may be acting to curb *Typha* expansion as the site ages. This is consistent with anecdotal evidence from site managers that in older created wetlands *Typha* density tends to decrease (pers. comm. S. Russell and L. Snead; VDOT). The applicability of the proposed model is based on only two years of data, therefore, in order to confirm that this is occurring, soil nutrient availability and expansion of *Typha* stand area and density would need to be measured annually in many created wetlands for a number of years.

Recommendations

The initial vegetation community in primary successional wetlands is often controlled by recruitment from surrounding wetlands. When a created forested wetland is constructed in an area in which the majority of adjacent wetland vegetation is associated with mature forested wetlands, the herbaceous propagule availability is much lower. Therefore, the seeds that do make it into the site are often from the weedy cosmopolitan species that can be found in nearby ditches and wet areas. These tend to be *Typha* spp., *Lythrum salicaria*, *Phragmites australis, Scirpus cyperinus, and Juncus effusus*. As a result of this trend, more effort should be made in the construction phase to establish a more diverse herbaceous wetland community, such as plantings and seedings over multiple years and by hand removal of known invasives, such as *L. salicaria* and *P. australis*.

If *Typha* and other vegetation in these sites are allowed to grow over many seasons, they may eventually remove and store enough P from the soil that it will lead to a P deficient system, which may effectively limit *Typha* expansion. When herbicide applications are used to control *Typha* populations, even with removal of aboveground biomass, the rhizomes, which are the main nutrient storage tissue, are killed and remain in the soil where they are eventually incorporated into soil TP. This may actually prolong the high P availability conditions favorable to *Typha* expansion, by effectively setting back the soil successional sequence. Therefore, based on the conclusions of this research it is likely that the expansion and density of the *Typha* stands will decrease over time as soil P availability decreases from storage in perennial biomass.

APPENDIX A: 2007 VEGETATION LIST AND IMPORTANCE VALUES

Appendix A Table 1. Plant species occurring in *Typha* and non-*Typha* stands at all sites (summer 2007), species names are accompanied by wetland indicator status, and duration. Dominant species within each stand are denoted by *.

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha	Sandy Bottom Typha	Sandy Bottom Non-Typha
ALISMATACEAE										
Alisma subcordatum Raf.	OBL	Perennial				0.84	5.79	0.75		
Sagittaria australis (J.G. Sm.) Small		Perennial		1.09	1.27	1.04				
Sagittaria latifolia Willd.	OBL	Perennial		3.87	0.61					
APIACEAE										
Hydrocotyle umbellata L.	OBL	Perennial		3.12	24.59*	16.79*				
Ptilimnium capillaceum (Michx.) Raf.	OBL	Annual			4.02	3.35	2.00	2.55		
Araceae										
Peltandra virginica (L.) Schott	OBL	Perennial	6.31	21.48*						

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha	Sandy Bottom Typha	Sandy Bottom Non-Typha
ASTERACEAE										
Bidens sp.				1.38		0.41				
Cirsium virginianum L. Michx	FACW	Biennial				0.47				
Eupatorium perfoliatum L.	FACW+	Perennial						0.88		
Mikania scandens (L.) Willd.	FACW+	Perennial				2.98	0.74	0.98		
Solidago canadensis L.	FACU	Perennial				0.43				
Symphyotrichum lateriflorum (L.) A.& D. Löve	FAC	Perennial				1.70	1.52	1.06		
BALSAMINACEAE										
Impatiens capensis Meerb.	FACW	Annual	0.77			1.67				
CYPERACEAE										
Carex crinita Lam.	OBL	Perennial					2.39	5.72		
Carex lurida Wahlenb.	OBL	Perennial		3.35	0.56	3.44	1.79	0.67		

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha	Sandy Bottom Typha	Sandy Bottom Non-Typha
CYPERACEAE										
Carex sp.			1.81		0.78	0.88	2.36	7.34		5.72
Carex vulpinoidea Michx.	OBL	Perennial						1.13		
Cyperus sp.				1.50		0.53				4.79
Eleocharis acicularis (L.) Roemer & J.A. Schultes	OBL	Annual/ Perennial	4.81	6.12					3.77	5.54
Eleocharis obtusa (Willd.) J.A. Schultes	OBL	Annual/ Perennial		4.95		1.03			14.92	14.59*
Eleocharis parvula (Roemer & J.A. Schultes) Link ex Bluff, Nees & Schauer	OBL	Annual/ Perennial			0.62				3.39	9.31
Eleocharis quadrangulata (Michx.) Roemer & J.A. Schultes	OBL	Perennial							13.98	8.02
Scirpus cyperinus (L.) Kunth	FACW+	Perennial			5.36	13.58*		3.60		
IRIDACEAE										
Iris versicolor L.	OBL	Perennial				0.86				

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha	Sandy Bottom Typha	Sandy Bottom Non-Typha
JUNCACEAE										
Juncus acuminatus Michx.	OBL	Perennial				1.30			4.32	14.93*
Juncus diffusissimus Buckl.	FACW	Perennial	0.93	2.34						
Juncus effusus L.	OBL	Perennial	1.85	4.40	7.16	10.34*	23.98*	50.96*		4.85
Juncus tenuis Willd.	FAC-	Perennial					1.26			
LYTHRACEAE										
Rotala ramosior L. Koehne	OBL	Annual	0.24	1.71						
Onagraceae										
Ludwigia palustris (L.) Ell.	OBL	Perennial				0.64				
Ludwigia repens J.R. Forst.	OBL	Perennial	0.77	2.74		0.52				
POACEAE										
Calamagrostis canadensis (Michx.) Beauv.	FACW+	Perennial			0.95	3.95				

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha	Sandy Bottom Typha	Sandy Bottom Non-Typha
POACEAE										
Eragrostis hypnoides (Lam.) B.S.P.	OBL	Annual					7.21	6.73	0.75	7.36
Eragrostis sp.								9.57		
Leersia oryzoides (L.) Sw.	OBL	Perennial			5.75	7.34*	7.68	3.01		
POLYGONACEAE										
Polygonum arifolium L.	OBL	Annual				3.44				
Polygonum hydropiperoides Michx.	OBL	Perennial		2.47	4.71	1.86	0.62			
Polygonum pensylvanicum L.	FACW	Annual						0.69		
Polygonum sp.				1.07	6.39	5.12				
Polygonum sagittatum L.	OBL	Annual/ Perennial				1.79	0.85			
PONTEDERIACEAE										
Pontedaria cordata L.	OBL	Perennial	20.93*	36.71*	6.41	1.25				

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha	Sandy Bottom Typha	Sandy Bottom Non-Typha
ROSACEAE										
Rubus argutus Link	FACU	Perennial				0.47				
RUBIACEAE										
Cephalanthus occidentalis L.	OBL	Perennial			3.44	2.68	0.73			
Galium trifidum L.	FACW+	Perennial			3.15	2.88	1.50	0.78		
SAURURACEAE										
Saururus cernuus L.	OBL	Perennial	2.41	0.69						
TYPHACEAE										
Typha spp. L.	OBL	Perennial	59.17*	1.00	24.23*	6.41	39.59*	3.58	58.87*	24.90*

APPENDIX B: 2006 WATER DEPTH AND VEGETATION COMMUNITY DATA

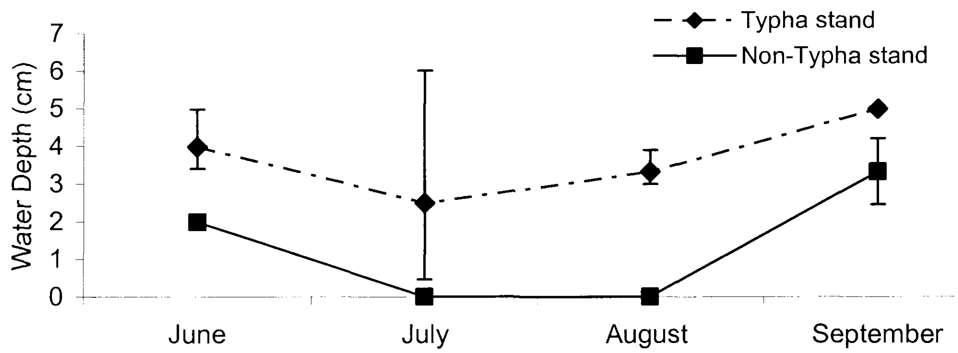
Appendix B Table 1: Mean (± 1 SE) Water depth data (cm) *Typha* stands Suffolk 2006 growing season (June to September).

Depth Measurement Replicates	June	July	August	September
Quadrat 1	5	5	3	5
Quadrat 2	3	0	4	5
Quadrat 3	4	3	3	5
Monthly Mean	4	3	3	5
Standard Deviation	1.0	3.5	0.6	0.0
Standard Error	0.6	2.0	0.3	0.0

Appendix B Table 2: Mean (± 1 SE) Water depth data (cm) Non-*Typha* stands Suffolk 2006 growing season (June to September).

Depth Measurement Replicates	June	July	August	September
Quadrat 1	2	0	0	3
Quadrat 2	2	0	0	5
Quadrat 3	2	0	0	2
Monthly Mean	2	0	0	3
Standard Deviation	0.0	0.0	0.0	1.5
Standard Error	0.0	0.0	0.0	0.9

Appendix B Figure 1. Mean (± 1 SE) monthly water depth Suffolk 2006 growing season (June to September).



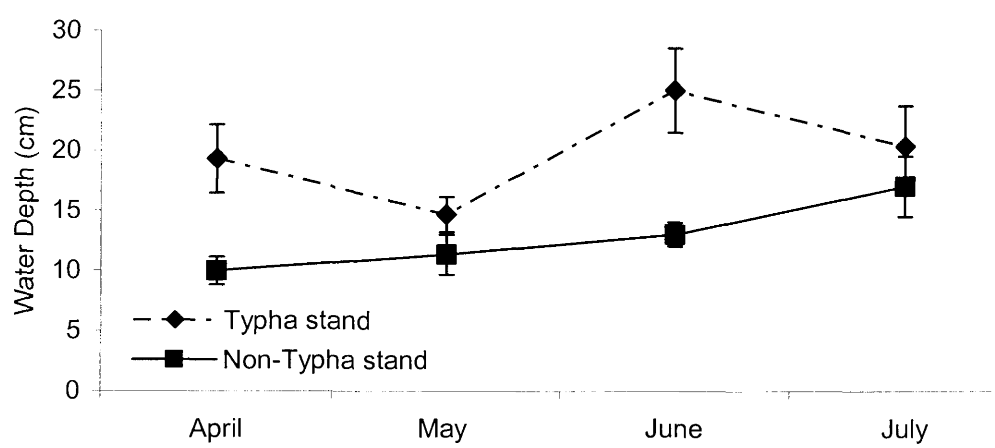
Appendix B Table 3. Mean (± 1 SE) Water depth data (cm) *Typha* stands Courtland East 2006 growing season (June to September).

Depth Measurement Replicates	June	July	August	September
Quadrat 1	16	12	10	27
Quadrat 2	17	17	12	18
Quadrat 3	25	15	22	16
Monthly Mean	19	15	25	20
Standard Deviation	4.9	2.5	6.1	5.9
Standard Error	2.8	1.5	3.5	3.4

Appendix B Table 4. Mean (± 1 SE) Water depth data (cm) Non-*Typha* stands Courtland East 2006 growing season (June to September).

Depth Measurement Replicates	June	July	August	September
Quadrat 1	12	13	12	19
Quadrat 2	10	8	12	12
Quadrat 3	8	13	15	20
Monthly Mean	10	11	13	17
Standard Deviation	2.0	2.9	1.7	4.4
Standard Error	1.2	1.7	1.0	2.5

Appendix B Figure 2. Mean (± 1 SE) monthly water depth Courtland East 2006 growing season (June to September).



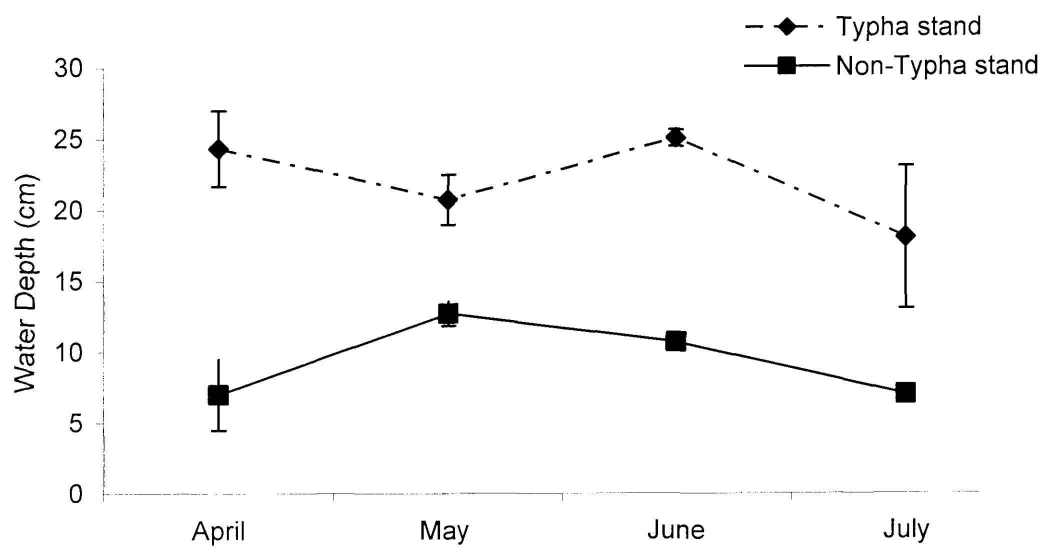
Appendix B Table 5. Mean (± 1 SE) Water depth (cm) data *Typha* stands Courtland West 2006 growing season (June to September).

Depth Measurement Replicates	June	July	August	September
Quadrat 1	19	24	26	28
Quadrat 2	27	20	24	13
Quadrat 3	27	18	25	13
Monthly Mean	24	21	25	18
Standard Deviation	4.6	3.1	1.0	8.7
Standard Error	2.7	1.8	0.6	5.0

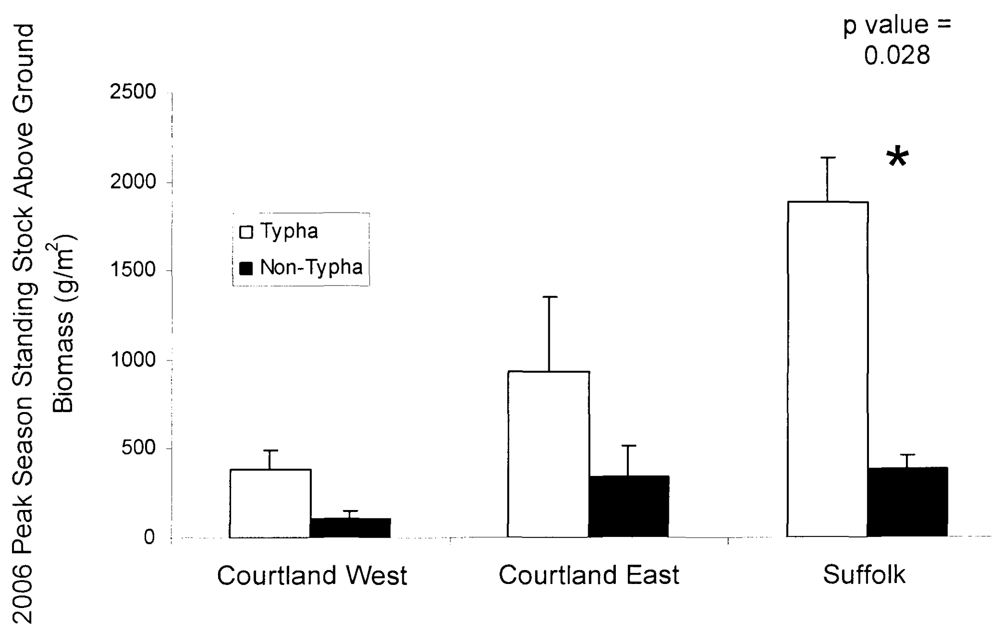
Appendix B Table 6. Mean (± 1 SE) Water depth data (cm) Non-*Typha* stands Courtland West 2006 growing season (June to September).

Depth Measurement Replicates	June	July	August	September
Quadrat 1	4	11	10	6
Quadrat 2	12	13	11	8
Quadrat 3	5	14	11	7
Monthly Mean	7	13	11	7
Standard Deviation	4.4	1.5	0.6	1.0
Standard Error	2.5	0.9	0.3	0.6

Appendix B Figure 3. Mean (± 1 SE) monthly water depth Courtland West 2006 growing season (June to September).



Appendix B Figure 4. 2006 mean (± 1 SE) peak season (August) standing stock above ground biomass, * indicates significant difference as indicated by t-test (α =0.05).



Appendix B Table 7. 2006 Shannon diversity index (H'), including results of statistical analysis of difference between *Typha* and Non-*Typha* stands, * indicates significant difference in H' as indicated by Hutcheson's modified t-test (α =0.05).

Sites	Typha Stand Shannon Diversity (H')	Non-Typha Stand Shannon Diversity (H')
Courtland West* p value = 0.0306	1.78	1.14
Courtland East* p value < 0.001	1.13	1.41
Suffolk* p value < 0.001	1.18	1.13

Appendix B Table 8. 2006 Species Richness (SR) including results of statistical analysis of difference between *Typha* and Non-*Typha* stands, * indicates significant difference in SR as indicated by t-test (α =0.05).

Sites	Typha stand Species Richness (SR)	Non-Typha stand Species Richness (SR)
Courtland West	4.08 ±0.26	4.00 ±0.49
Courtland East	2.25 ±0.18	2.17 ±0.41
Suffolk	2.58 ±0.23	2.17 ±0.30

Appendix B Table 9. Plant species occurring in *Typha* and non-*Typha* stands at all sites 2006 growing season (June to September), species names are accompanied by wetland indicator status, and duration. Dominant species within each stand are denoted by *.

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha
Acoraceae								
Acorus clamus L.	OBL	Perennial				0.83		
Alismataceae								
Sagittaria latifolia Willd.	OBL	Perennial		3.94	2.15	2.07		
Apiaceae								
Hydrocotyle umbellata L.	OBL	Perennial	1.52	9.69	32.52 *	11.10		
Ptilimnium capillaceum (Michx.) Raf.	OBL	Annual			5.64	2.81		
Araceae								
Peltandra virginica (L.) Schott	OBL	Perennial	19.12	13.37	1.00			

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha
CYPERACEAE								
Carex crinita Lam.	OBL	Perennial		1.33		4.69	4.16	5.72
Carex lurida Wahlenb.	OBL	Perennial				2.59	5.54	1.68
Eleocharis acicularis (L.) Roemer & J.A. Schultes	OBL	Annual/ Perennial		2.78			1.57	
Eleocharis obtusa (Willd.) J.A. Schultes	OBL	Annual/ Perennial				3.10		
Scirpus cyperinus (L.) Kunth	FACW+	Perennial			1.01	36.38*	1.77	
JUNCACEAE								
Juncus acuminatus Michx.	OBL	Perennial					1.16	2.66
Juncus effusus L.	OBL	Perennial	3.14		5.96	17.51*	32.64*	68.52*
POACEAE								
Eragrostis hypnoides (Lam.) B.S.P.	OBL	Annual		1.33				15.06

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha
POACEAE								
Leersia oryzoides (L.) Sw.	OBL	Perennial			5.00	4.97		
POLYGONACEAE								
Polygonum hydropiperoides Michx.	OBL	Perennial			8.95	4.88		2.19
Polygonum pensylvanicum L.	FACW	Annual		1.39				
PONTEDERIACEAE								
Pontedaria cordata L.	OBL	Perennial	19.39	60.22*	1.39			
RUBIACEAE								
Galium trifidum L.	FACW+	Perennial				4.15		
RANUNCULACEAE								
Ranunculus sp.								1.17

Species	Indicator	Duration	Courtland East Typha	Courtland East Non-Typha	Courtland West Typha	Courtland West Non-Typha	Suffolk Bypass Typha	Suffolk Bypass Non-Typha
SAURURACEAE								
Saururus cernuus L.	OBL	Perennial		2.34				
TYPHACEAE								
Typha spp. L.	OBL	Perennial	56.82*	3.60	32.10*	3.99	53.16*	1.50
CUPRESSACEAE								
Taxodium distichm (L.) L.C. Rich.	OBL	Perennial						1.50

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