

**Hybrid Cattail (*Typha x glauca*) Growth and Nutrient Content
along a Water Depth Gradient in Two Prairie Marshes**

By

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Abstract

This study examined how growth and nutrient content of hybrid cattail (*Typha x glauca*) responded to water depth and hydroperiod in Oak Hammock Marsh and Delta Marsh, Manitoba. Above- and belowground biomass was collected along a water depth gradient at Oak Hammock Marsh and analyzed for total phosphorus, total nitrogen, total Kjeldahl nitrogen, shoot height, and density. Shoot height and biomass allocation exhibited a plastic response to increasing water depth, indicating that hybrid cattail can adjust to environmental conditions associated with deeper water. Nitrogen uptake increased concomitantly with phosphorus but was disproportionately allocated to aboveground tissue. Archival data from experimental wetland cells in Delta Marsh subject to either one or two years of drawdown showed that drawdown duration did not result in different hybrid cattail aboveground biomass or phosphorus and nitrogen content. This is likely because the wetlands had reached the degenerating stage of the prairie marsh wet-dry cycle only four years after drawdown. Hybrid cattail was able to maintain productivity from upland to 55 cm of standing water which allows for latitude in wetland design and water level management. Quick progression to the degenerating stage presents a challenge to wetlands managed for nutrient removal because of decline in productivity and necessity for frequent drawdowns.

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CHAPTER 1 – Literature Review

1.1. Wetlands

What is a Wetland?

While the specifics of wetland definitions vary, consensus is the land must be wet, particularly during the growing season, such that its biogeochemical processes and characteristics are different than that of dry land and support hydrophytes as the dominant vegetation. The National Wetlands Working Group (1997) of Canada defines wetlands as “land that is saturated with water long enough to promote wetland or aquatic processes as indicated by poorly drained soils, hydrophytic vegetation and various kinds of biological activity which are adapted to a wet environment”.

Cowardin et al. (1979) developed a nation-wide comprehensive classification system of wetlands that is widely used in the United States. They define wetlands as lands that are “transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water”, adding that wetlands must at some point be dominated by hydrophytic vegetation, have undrained hydric soil, and/or a nonsoil substrate that is saturated or covered by shallow water at some time during the annual growing season.

The Ramsar Convention on Wetlands of International Importance has a very broad definition of wetlands, including all areas of “marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters” (Ramsar, 1987). By using such an inclusive definition, the Ramsar

Convention and its members are able to include a greater variety and larger area of ecosystems as wetlands worthy of protection (Scott & Jones, 1995).

Types of Wetlands

Bowden (1987) lists climate, hydrology, geomorphology, and vegetation as the four parameters that most strongly shape the formation of a wetland. Differences in these variables, and others such as sediment and water chemistry, lead to wetlands with vastly different defining characteristics. The result is an array of different wetland types.

Recognizing the similarities and dissimilarities of different wetland types is necessary in order to establish a cohesive knowledge base on the importance of wetlands, how they function and respond to natural or anthropogenic disturbances, and how best to restore, preserve and manage them. To meet this need, many classification systems have been developed. However, systems often place wetland characteristics in different hierarchical order, resulting in wetland types that cannot always be equated to classifications of other systems.

The Canadian Wetland Classification System (CWCS) was developed by the National Wetlands Working Group (NWWG, 1997) to provide a user-friendly standardized way of classifying wetlands in Canada. The system recognizes two broad categories of wetland: peat-forming organic wetlands and non-peat-forming mineral wetlands. CWCS is a three-tier hierarchical system that divides wetlands into class, form, and type.

Classes are identified based on properties that reflect the formation of the wetland and its current environment. There are five classes: bogs, fens, swamps, marshes, and shallow water. Bogs are peat-forming organic wetlands that receive water exclusively from

precipitation and are dominated by bryophytes, particularly *Sphagnum* moss, and graminoids. Fens are also peat-forming but are more heavily dominated by graminoids than bryophytes and are in contact with nutrient-rich groundwater. Peat-forming wetlands dominated by trees, shrubs and forbs are classified as swamps. Swamps may also be non-peat forming mineral wetlands, characterized by slow moving nutrient-rich groundwater, periodic standing water, and woody vegetation. In contrast, marshes are mineral wetlands that have periodic or persistent standing water which is neutral to slightly alkaline and nutrient-rich, and are dominated by graminoids, shrubs, forbs or emergent vegetation. Mineral wetlands with large expanses of water up to 2 m deep that is persistent for at least most of the year and contain mostly submerged or floating aquatic plants are classified as shallow water wetlands.

CWCS classes are divided into forms based on surface morphology, surface pattern, water type, and morphology characteristics of underlying mineral soil. Some forms are further divided into subforms, and may also be applied to more than one class. Lastly, forms and subforms are divided into types, and occasionally subtypes, based on physiognomic characteristics of the vegetation communities. These may also apply to more than one class. The result of CWCS is over 85 different varieties wetlands.

Cowardin et al. (1979) developed a system for wetland and deepwater classification to standardize wetland identification in the USA, though their system has also received international use. Like the CWCS, it is a hierarchical system but begins by using hydrologic, geomorphologic, chemical, and biological factors to divide wetlands into one of five systems: marine, estuarine, riverine, lacustrine, and palustrine. These are further divided into subsystems based on hydrological characteristics such as water depth and

tidal influence. Subsystems are then assigned to a class on the basis of dominant vegetation, substrate, or water regime. There are a total of 55 classes.

1.2. North American Prairie Marshes

Many different types of wetlands exist in the mid-continental prairies of North America, but perhaps the most notable are its freshwater prairie marshes. Prairie marshes range from small potholes to massive lacustrine marshes (Murkin et al., 2000b). They are characterized by alternating flooding and drying cycles that create very dynamic ecosystems (Shay & Shay, 1986). Thus the hydrology of prairie marshes is an integral component to their formation and continued existence.

Prairie potholes, also called glacial potholes, kettles, or sloughs, were formed during the Wisconsin glaciation, when the retreating Laurentide Ice Sheet left depressions of various sizes in the otherwise flat topography of the prairies. Prairie potholes range from less than half to several hectares in size (Richardson, et al., 1994).

These depressions are most abundant in the central Interior Plains in an area called the Prairie Pothole Region (PPR) (Figure 1). It includes southern Alberta and Saskatchewan, southwestern Manitoba, northeastern Montana, northern and east-central North Dakota, eastern South Dakota, western Minnesota, and northwestern Iowa (Stewart & Kantrud, 1971). PPR depressions accumulate snowmelt water in spring and because of poor drainage and connectivity, and retain water during at least part of the growing season, creating a wetland environment (Richardson, et al., 1994). The Canadian Wetland Classification System identifies most prairie potholes as isolated basin marshes or occasionally linked basin marshes if they have channelized inlets and outlets (NWWG,

1997). Also common in the prairies are lacustrine marshes located along the shores of permanent open water bodies and lakes (NWWG, 1997). An estimated 23% of land in the Prairie Pothole Region is wetland (Euliss et al., 2006).



Figure 1. Prairie Pothole Region of North America.

Classification of Prairie Marshes

Classification systems such as the Canadian Wetland Classification System (NWWG, 1997) and that of Cowardin et al. (1979) can provide nationally cohesive identification of wetland types, but they are often too broad for use at a smaller regional scale, such as the Prairie Pothole Region. The CWCS key identifies prairie potholes as isolated or linked

basin marshes, and provides some modifiers to further describe them. However, small variations in key features, such as size, hydrology, and water chemistry, may produce prairie potholes that, on a subtle scale, are very different and should not be identified as the same.

Stewart & Kantrud (1971) addressed this issue by creating the *Classification of Natural Ponds and Lakes in the Glaciated Prairie Region*. Their system begins by placing a prairie wetland into one of seven classes, using the presence and distributional pattern of various vegetation zones, with particular focus on which vegetation zone dominates the deepest part of the basin. The basis of these zones is differences in community structure and life form of wetland plant species as influenced by water depth tolerances. There are seven different zones including grass and sedge-dominated prairie and wet meadow zones, emergent vegetation-dominated shallow- and deep-marsh zones, submerged vegetation-dominated open water zone, and an intermittent alkali zone lacking all forms of vegetation. Classes are further divided into as many as five subclasses using distinct wetland plant assemblages that reflect the salinity of standing water. Stewart & Kantrud (1971) provide a detailed list of wetland species found in each vegetation zone, class, and subclass, to aid in prairie wetland classification.

Climate and Environmental Conditions

Bowden (1987) identifies climate as the most important variable in wetland formation. Precipitation must exceed evapotranspiration in order for there to be a lasting water supply in some marshes. Where evapotranspiration exceeds precipitation, marsh water levels may decrease or dry up entirely (Shay & Shay, 1986). Temperature can influence

marsh productivity and nutrient cycling through its effect on the kinetics of various vegetation and microbial biochemical processes (Bowden, 1987).

The Prairie Pothole Region is mid-continental and temperate. There are no bogs or fens in the region because high summer temperatures and insufficient rainfall prevent the formation of peat (Zoltai, 1987). The southeast extreme of the PPR in north-central Iowa experiences mean temperatures of 23.5 and -8.0°C in July and January, respectively, and receives approximately 780 mm of annual precipitation, mostly in the spring (van der Valk & Davis, 1978). At the northeastern extent of the PPR, in south-central Manitoba, mean temperatures range from 19.9°C to -16.4°C in July and January, respectively, and annual precipitation is 550.1 mm, mostly as rainfall (Environment Canada, 2015c). Towards the northwestern edge of the PPR in southeastern Alberta mean temperatures in July and January are 20°C and -8.4°C, respectively, and annual precipitation is 322.6 mm, mostly as rainfall (Environment Canada, 2015b). Fluctuations in precipitation tend to be cyclical, alternating between high and low precipitation extremes (Shay & Shay, 1986).

Hydrology

After climate, hydrology is the next more important variable to wetland formation (Bowden, 1987). In addition to being essential to the growth and function of flora and fauna, water entering a marsh carries with it necessary nutrients and sediments (Johnston, 1991), but can also flush nutrients from a marsh (Bowden, 1987).

Water sources in the prairies include precipitation, groundwater discharge, and surface water from overland flooding, runoff, streams / rivers, and lakes (Johnston, 1991;

Kantrud et al., 1989). In systems exposed to human activity, wastewater discharge may be a source of water. Similar routes explain water loss from marshes; evapotranspiration, groundwater recharge, and surface outflow into connecting streams, lakes, and rivers (Johnston, 1991; Kantrud et al., 1989). Seasonal variation may affect water input and output schemes (Shay & Shay, 1986).

Most isolated prairie potholes depend on overland spring flooding from snowmelt and precipitation during the growing season to supply water. These marshes may experience a water deficit if evapotranspiration exceeds precipitation, as it does in much of the prairies (Shay & Shay, 1986). If in contact with groundwater, some potholes may have their water levels replenished by its discharge (Shay & Shay, 1986). Linked basin marshes may receive a continuous supply of water from the streams and rivers to which they are connected. Similarly, lacustrine marshes are in constant contact with a water supply.

Climate strongly influences prairie marsh hydrology as most water sources are ultimately precipitation-dependent. Cyclical fluctuation between high and low precipitation extremes (Shay & Shay, 1986), leads to a cyclical fluctuation in water supply, giving rise to the characteristic wet-dry cycle of prairie pothole and lacustrine marshes. The fluctuation between low and high water levels, termed hydroperiod, affects water and sediment chemistry, primary production, vegetation composition and distribution, and nutrient budgets (Kantrud et al., 1989; Murkin et al., 2000b; Shay & Shay, 1986).

Water and Sediment Chemistry

Prairie marsh water chemistry is influenced by geology, hydrology, and climate. Surface water and groundwater entering a marsh brings with it nutrients and sediment collected

from the surrounding soils (Johnston, [1991](#); Shay & Shay, [1986](#)). Agriculture runoff and wastewater discharge can introduce large amounts of nutrients, creating a eutrophic system.

Prairie marshes are freshwater though some can become slightly brackish (Shay & Shay, [1986](#)). Salinity is strongly influenced by water source; in general precipitation is low, surface water is intermediate, and groundwater is high in dissolved salts (Kantrud et al., [1989](#)). Groundwater salinity depends on the characteristics of the underlying substrate and groundwater flow (Kantrud, et al., [1989](#); Shay & Shay, [1986](#);). PPR groundwater in the prairies is dominated by calcium, sodium, and magnesium sulfate salts (Shay & Shay, [1986](#)).

Hydroperiod and seasonal fluctuation in water level can alter a prairie marsh water chemistry (Shay & Shay, [1986](#)). For example, prairie marshes that experience a water deficit when evapotranspiration exceeds precipitation during the growing season may experience an increase in solute concentration as water volumes decrease (Liefers & Shay, [1983](#)).

When the Laurentide Ice Sheet retreated at the end of the Wisconsin glaciation episode 10,000 years ago, it deposited sands, silts and clay on the underlying sedimentary rock of the Prairie Pothole Region (Galatowitsch & van der Valk, [1996](#); Kantrud et al., [1989](#); Shay & Shay, [1986](#)). Prairie marshes are seasonally or permanently flooded and thus develop hydric soil conditions. PPR soils are typically mineral gleysols high in calcium, resulting in a neutral to slightly alkaline soil pH (Galatowitsch & van der Valk, [1996](#); Lindgren, [2001](#); Walker, [1965](#)). Accumulation of plant matter on the sediment surface

may create a thin layer of peat, under which is a layer of permanently reduced gleysols (Ponnamperuma, [1972](#)).

Hydric soil and reduced gleysols are the result of net consumption of oxygen at the marsh soil surface (Dunne & Reddy, [2005](#)). Oxygen diffusion through the water column and in the soil pore water is slow while the oxygen demand by soil microbial activity is high, resulting in net consumption of oxygen (Brix, [1994](#); Dunne & Reddy, [2005](#)). Thus water saturated soil becomes hypoxic or anoxic, promoting anaerobic processes and reduced conditions (Brix, [1994](#); Gosselink & Turner, [1978](#)). There may be a thin oxidized layer at the soil/water interface where aerobic processes can occur (Dunne & Reddy, [2005](#)). Oxygen availability and reduced conditions influence bioavailability of some nutrients, such as N and P (Gosselink & Turner, [1978](#)).

Nitrogen and Phosphorus Cycling in Marsh Sediments

N and P are considered essential elements for the health of all plants, including emergent macrophytes, and are classified as macronutrients because they are required in large amounts relative to other nutrients and minerals. These nutrients are of particular interest because of their anthropogenic uses and role in eutrophication of water bodies.

N and P bioavailability and cycling depends on a variety of abiotic and biotic factors including internal and external input, climate, hydrology, geomorphology, sediment chemistry (e.g. pH, redox potential, nutrient concentrations, etc.), and vegetation (Bowden, [1987](#); Koerselman et al., [1993](#); Vymazal, [2007](#)). For example, mobility of N in marshes is impeded when surface and subsurface water flow is reduced, which often occurs when evapotranspiration exceeds precipitation (Bowden, [1987](#)). Temperature

influences biochemical kinetics, and thus regulates plant and microbial nutrient processing rates (Bowden, [1987](#)). Hydrologic inputs carry varying amounts of nutrients into a wetland ecosystem, but outputs may flush them from the system (Bowden, [1987](#)). Uptake, sequestration, and release of nutrients by plants influence the internal dynamics of nutrient cycling in wetlands. Changes in environmental conditions can release nutrients already in the wetland ecosystem, in a process termed “internal eutrophication” by Koerselman et al. ([1993](#)), thus increasing their bioavailability.

N enters wetland ecosystems through wet and dry atmospheric deposition, overland flooding / runoff, subsurface flow, and N-fixation (Bowden, [1987](#); Galloway et al., [2003](#)). Most N in wetlands is found in the sediments, and much of this N is in forms unavailable for plant uptake (Bowden, [1987](#)). N is available to emergent macrophytes only in the dissolved inorganic forms of nitrate (NO_3^-) and ammonium (NH_4^+), both of which can be found in pore water to varying degrees. Because wetland soils are hydric, most inorganic N exists as ammonium (Bowden, [1987](#)), which can be taken up by plants or adsorbed to sediment particles.

Ammonium is made available through N fixation, where atmospheric N (N_2) is converted to ammonium by N-fixing bacteria, and ammonification (aka mineralization), where bacteria and fungi breakdown organic matter, releasing the organic N as ammonium. N-fixation can occur under oxic and anoxic conditions (Vymazal, [2007](#)). Microbial ammonification can occur by aerobic or anaerobic processes (Crumpton & Goldsborough, [1998](#); Vymazal, [2007](#)). Microorganisms involved in the ammonification process or inhabiting the decomposing organic matter may take up the inorganic N, converting it back to organic N, in a process called immobilization. Microbial

immobilization occurs under aerobic conditions (Bowden, [1987](#)). The balance between microbial ammonification and immobilization determines the amount of ammonium made available through decomposition (Bowden, [1987](#); Crumpton & Goldsborough, [1998](#)).

Under high pH conditions (>10) ammonium can be converted to gaseous ammonia (NH_3), which is then lost to the atmosphere in a process called volatilization (Ambler et al., [2001](#)). Ammonium may adsorb to inorganic sediment particles, at which point it is not available for uptake by plants. It will desorb if ammonium concentrations in the pore water declines, such that an equilibrium between adsorbed and desorbed ammonium exists (Vymazal, [2007](#)). Bioavailable ammonium is assimilated by plants under aerobic conditions (Ambler et al., [2001](#)).

Nitrate is made available through the oxidative process of nitrification, in which ammonia or ammonium not taken up by plants or adsorbed to sediments is oxidized to nitrite (NO_2^-), which is then oxidized to nitrate (Ambler, et al., [2001](#); Bowden, [1987](#); Vymazal, [2007](#)). This process is performed by nitrifying bacteria in the thin aerobic soil/water interface and aerobic rhizosphere, and depends on the availability of ammonium, oxygen, and carbon dioxide (CO_2) (Vymazal, [2007](#)). It is also influenced by pH, temperature, and lack of available P (Bowden, [1987](#)). By definition, wetland soils exist under oxygen stress. Consequently, the reductive process of denitrification, in which nitrate is reduced to nitrous oxide (NO_2) or atmospheric N by anaerobic bacteria, is favoured leading to low amounts of nitrite and nitrate in the sediment (Bowden, [1987](#)). The anoxic conditions of most wetlands makes them highly efficient at denitrification (Galloway et al., [2003](#)). High levels of nitrate can encourage the process of

denitrification. Products of denitrification are lost from the ecosystem to the atmosphere (Bowden, [1987](#)). Bioavailable nitrate is assimilated by plants under aerobic conditions (Ambler et al., [2001](#)).

P enters a wetland through wet and dry atmospheric deposition, overland flooding, and subsurface flow. Surface-applied manure and fertilizer provide a readily available source of P where surface waters drain into wetlands (Young & Ross, [2001](#)). Wetland P can be categorized as dissolved inorganic P (DIP), dissolved organic P (DOP), particulate inorganic P (PIP), and particulate organic P (POP) (Dunne & Reddy, [2005](#)). Most P in a wetland is organic, but only pore water dissolved inorganic P, as phosphate (PO_4^{3-}), is available for plant uptake (Vymazal, [2007](#)). Its availability is strongly governed by calcium in alkaline mineral wetland soils, and iron or aluminium in acidic mineral wetland soils, as well as pH and redox potential (Dunne & Reddy, [2005](#)).

Phosphate (PO_4^{3-}) reacts with metallic cations to form a solid precipitate under aerobic conditions and in the presence of abundant P and metallic ions. In alkaline sediments it reacts with calcium (Ca^{2+}), and in acidic sediments it reacts with iron (Fe^{3+}) or aluminium (Al^{3+}) (Dunne & Reddy, [2005](#)). This process can drastically reduce the amount of bioavailable P. However, iron oxides are reduced and P solubility increases under anaerobic conditions, regardless of pH levels, which facilitates dissolution of precipitated P thereby increasing pore water P (Aldous et al., [2005](#); Dunne & Reddy, [2005](#); Young & Ross, [2001](#)).

Dissolved inorganic P in pore water can adhere to and/or penetrate the surface of sediment mineral surfaces, through the processes of adsorption and absorption,

respectively (Vymazal, [2007](#)). Solid-phase P is not available for plant uptake. However, these processes can be reversed through desorption if the concentration of pore water P is low (Dunne & Reddy, [2005](#)) or under anoxic conditions (Young & Ross, [2001](#)). The rates of sorption and desorption are dynamic and depend on pore water and solid-phase P concentrations, such that a net flux of P from one phase to the other will occur until an equilibrium is reached (Dunne & Reddy, [2005](#)). Reduced wetland soils tend to adsorb more P but with a weaker bond than oxidized soils (Dunne & Reddy, [2005](#)).

Under aerobic conditions, decomposition of organic matter (i.e. mineralization) releases P (Aldous et al., [2005](#); Vymazal, [2007](#)). However, released P may become immobilized if taken up by microorganisms (Qualls & Richardson, [2000](#)). Particulate P may undergo sedimentation. Some organic P compounds, such as nucleic acids and phospholipids, can undergo sorption to clay or soil organic matter, or form complexes with metallic cations (Dunne & Reddy, [2005](#)).

Bioavailable N is taken up by plants and incorporated into amino acids, proteins, nucleotides for DNA and RNA, nucleic acids, chlorophylls, and coenzymes. P taken up by plants is used in proteins, nucleic acids, coenzymes, phospholipids which form cell and organelle membranes, and for energy transfer in the form of adenosine triphosphate (ATP) (Dunne & Reddy, [2005](#)). Translocation of N and P from senescing plant tissue to storage tissue conserves some of the assimilated organic N and P (Bowden [1987](#); Dunne & Reddy, [2005](#)). Sharma et al. ([2006](#)) found that narrow-leaf cattail (*Typha angustifolia*) translocated 45-48% and 37-45% of its shoot N and P, respectively, to its rhizomes during senescence. However, leaching of water soluble N and P compounds is known to occur during senescence (Dunne & Reddy, [2005](#)). Sharma et al. ([2006](#)) found that *T.*

angustifolia released 4.6 g/m² and 0.8 g/m² of N and P, respectively, from dead shoots into the water after its senescence. Accumulation of leaf litter in wetlands leads to the formation of peat which acts as long-term nutrient sink (Dunne & Reddy, [2005](#); Vymazal, [2007](#)). Soluble N and P can be lost from the wetland where hydrological regimes include an output, though losses tend to be small (Bowden, [1987](#)).

Marsh Vegetation

Wetland plants are those that have adapted to growing in aquatic environments and/or the water-saturated, anaerobic conditions of wetland hydric soils. The presence of these plants is often a defining characteristic of wetlands, while the dominant species and community composition can help identify wetland type.

While many researchers consider only vascular plants when discussing marsh vegetation, it is important to note that non-vascular producers such as bryophytes and algae play an important role in productivity and nutrient cycling. Here, macrophyte will be used to refer to aquatic vascular plants.

Macrophytes are often categorized according to life form traits, and water depth and salinity tolerances (Shay & Shay, [1986](#); Spence, [1982](#); Stewart & Kantrud, [1971](#)). Different species can also be grouped together according to zones, such as those described by Stewart & Kantrud ([1971](#)), which reflect position along a moisture gradient based on life form and flood tolerance (Shay & Shay, [1986](#)).

There are five general macrophyte life forms based on attachment and location relative to the water surface: free-floating submerged, free-floating on the water surface, attached submerged, attached floating-leaved, and attached emergent macrophytes. Free-floating

submerged macrophytes common to prairie marshes include hornworts (*Ceratophyllum* spp.), water milfoil (*Myriophyllum sibiricum*), and the carnivorous common bladderwort (*Utricularia vulgaris*), which float submerged near the water surface. Duckweed (*Lemna* spp.) is a common prairie marsh macrophyte that floats freely on the water surface. Rooted macrophytes with no floating or emergent leaves found in prairie marshes include sago pondweed (*Stuckenia pectinata* syn. *Potamogeton pectinatus*) and sheathed pondweed (*Stuckenia vaginata* syn. *Potamogeton vaginatus*). Some attached submerged species may occasionally become uprooted and free-floating, such as Canadian waterweed (*Elodea canadensis*). Attached macrophytes with floating leaves commonly seen in prairie marshes are water lilies (*Nuphar* spp.) and broad-leaved pondweed (*Potamogeton natans*). Emergent macrophytes are rooted in sediment that may be saturated or flooded for part or all of the growing season, and have leaves that extend above the water surface. Cattail (*Typha* spp.), bulrush (*Schoenoplectus* spp., *Bolboschoenus* spp., and *Scirpus* spp.), sedges (*Carex* spp.), rushes (*Juncus* spp.), common reed (*Phragmites australis*), and whitetop grass (*Scolochloa festucacea*) are common in prairie marshes.

Stewart & Kantrud (1971) and Millar (1973) define similar zonation of prairie marsh plants according to water-depth and flood tolerances. The wet meadow zone is typically flooded during spring only, for three to four weeks, and contains grasses, some sedges, and forbs (Shay & Shay, 1986). The shallow marsh zone is inundated until late-summer and contains emergent macrophytes of intermediate height, such as whitetop grass (*Scolochloa festucacea*) and wheat sedge (*Carex atherodes*) (Millar, 1973). The deep marsh zone has standing water during the entire growing season and occasionally year-

round. It includes taller emergent macrophytes such as cattail (*Typha* spp.) and bulrush (*Schoenoplectus* spp., *Bolboschoenus* spp., *Scirpus* spp.), and some submerged macrophytes. The shallow open water zone and open alkali zone are permanently flooded. Emergent macrophytes are absent and submerged macrophytes such as water milfoil (*Myriophyllum exalbescens*), hornworts (*Ceratophyllum demersum*), and pondweeds (*Potamogeton* spp.) dominate (Millar, [1973](#)).

Shay & Shay ([1986](#)) consider the emergent zones of prairie marshes to be the most important for classification, productivity, and nutrient cycling.

1.3. Prairie Marsh Emergent Macrophytes

1.3.1. Adaptations to the Prairie Marsh Environment

Prairie marsh emergent macrophytes face several major challenges including reduced light in deep water for photosynthesis and an anaerobic sediment environment with limited oxygen availability for respiration, and limited carbon dioxide and mineral nutrient availability for metabolism (Guntenspergen et al., [1989](#)). Anaerobic sediment conditions may also lead to a potentially toxic environment (Brix, [1994](#)). Adaptations to these challenges can be morphological and/or physiological.

Many emergent macrophytes possess an internal lacunal system that transports air to the rhizomes, roots, and surrounding anaerobic sediment (Brix, [1994](#); Kozlowski, [1984](#); Vretare & Weisner, [2000](#)). The system consists of large internal air spaces (i.e. lacunae) that extend continuously from openings in the aerial leaves (i.e. stomata) to the rhizomes and roots. Air is first drawn in through stomata, then transported down into the rhizomes

and roots via the lacunal system, before being exhausted from a different part of the plant, often broken culms, than through which it entered (Brix, 1994).

Transport of oxygen and other gases through the lacunal system may be by passive molecular diffusion or, more often, convection (Brix, 1994). Convective flow results from differences in temperature or humidity between the air inside and outside the plant. It may also result from higher velocity wind blowing across upright broken dead culms (i.e. standing dead) in the upper canopy, resulting in air being drawn into broken culms in the lower canopy where wind velocity is lower (Brix, 1994). Retention of standing dead in the form of broken culms is therefore an essential adaptation to survival in prairie marshes for emergent macrophyte species that demonstrate this type of convective flow, such as the common reed (*Phragmites australis*) (Brix, 1994).

Lacunal system size is dependent on species, but it can occupy up to 60% of the total tissue volume in some emergent macrophytes (Brix, 1994). It also functions as structural support and, as a non-living tissue, helps reduce metabolic costs (Guntenspergen et al., 1989).

Air reaching the rhizomes provides the oxygen necessary for any cellular respiration activities. Oxygen leaks out of the roots and into the rhizosphere, oxygenating it and enabling aerobic decomposition of organic matter and growth of nitrifying bacteria, thus increasing the bioavailability of N in the rhizosphere (Brix, 1994; Kozłowski, 1984). The oxygen also oxidizes reduced toxic compounds such as ferrous and manganous ions into less harmful compounds (Kozłowski, 1984).

Many emergent macrophyte species including cattail (*Typha* spp.), bulrush (*Schoenoplectus lacustris* and *Bolboschoenus maritimus*), and common reed (*Phragmites australis*), have been found to produce taller shoots and/or leaves when growing in deeper water (Coops et al., [1996](#); Grace, [1989](#); Grace & Wetzel, [1982](#); Haslam, [1970](#); Lieffers & Shay, [1981](#); Squires & van der Valk, [1992](#); Waters & Shay, [1990](#);). It is thought that this may be to maintain a sufficient portion of tissue above the water surface for photosynthesis and gas exchange.

1.3.2. Functions in the Prairie Marsh Ecosystem

Emergent macrophytes provide many services, directly and indirectly, to the prairie marsh ecosystem.

Oxygen leaked into the sediment from emergent macrophyte roots creates a suitable environment for the growth of nitrifying bacteria (Brix, [1994](#); Kozlowski, [1984](#)). Submerged portions of culms and leaves provide a surface for periphyton (Brisson & Chazarenc, [2009](#); Brix, [1994](#)), and therefore indirectly provide a food source for animals such as seed shrimp (Ostracoda). Voigts ([1976](#)) found greater numbers of aquatic invertebrates in the emergent macrophyte zone than in areas of open water. Some species, such as seed shrimp (Ostracoda) and fingernail clams (*Sphaerium* spp.), prefer the emergent macrophyte zone to open water (Voigts, [1976](#)).

Emergent macrophytes in deeper water, such as cattail (*Typha* spp.) and bulrush (*Schoenoplectus*, spp., *Bolboschoenus* spp., *Scirpus* spp.), offer favourable predator / prey conditions for small fish like yearling yellow perch (*Perca flavescens*) (Suthers & Gee, [1986](#)). Many waterfowl, especially dabbling ducks such as mallard (*Anas platyrhynchos*)

and blue-winged teal (*Anas discors*), feed in the protection of sparse emergent macrophyte stands (Burger, 1985; Kantrud, 1986).

Emergent macrophyte foliage is used by many species of waterfowl as a food source or nest material (Brix, 1994; Kantrud, 1986). Red-winged blackbirds (*Agelaius phoeniceus*) build their nests in the emergent macrophyte canopy using leaves often from cattails (*Typha* spp.) (Burger, 1985). Grebes build their nests on the water using dead emergent macrophyte foliage, often in areas of submerged or barely emergent bulrush (*Schoenoplectus*, spp., *Bolboschoenus* spp., *Scirpus* spp.) or cattail (*Typha* spp.) standing dead (Burger, 1985). Nests of Franklin's gull (*Leucophaeus pipixcan*), coots (*Fulica* spp.), ruddy duck (*Oxyura jamaicensis*), mallard (*Anas platyrhynchos*), and blue-winged teal (*Anas discors*) are often built on the water surface and attached to dead emergent macrophyte culms (Burger, 1985).

Muskrats (*Ondatra zibethica*) use emergent macrophytes like cattail (*Typha* spp.) for food and to construct their dens (Connors et al., 2000).

Emergent macrophytes can prevent wind and wave action from stirring up sediments, which would increase turbidity and consequently reduce light availability for submerged macrophytes (Brisson & Chazarenc, 2009; van der Valk & Davis, 1978). Aerial portions of emergent macrophytes can reduce the amount of light in the water column, preventing phytoplankton blooms (van der Valk & Davis, 1978).

Standing dead from previous growing seasons provides cover for migratory waterfowl arriving in the spring (Burger, 1985) and, once covered with snow, insulates the marsh waters and sediment (Brisson & Chazarenc, 2009; Brix, 1994).

1.3.3. Prairie Marsh Factors that Affect Growth and Nutrient Content

Emergent macrophyte growth performance and nutrient concentration can be influenced by a variety of environmental variables, including water depth, hydroperiod, and sediment chemistry. The response of different species is dependent on their morphological and physiological adaptations. Consequently, certain environmental conditions may favour one emergent macrophyte species over another, and different species may exhibit opposite responses to the same environmental conditions.

Water Depth

Emergent macrophytes typically exhibit a maximum biomass over a range of water depths, but reduced biomass in shallower and deeper water outside that range (Bedish, 1967, Squires & van der Valk, 1992). Reduced biomass in shallower water reflects their moisture requirement (Bedish, 1967) while reduced biomass in deeper water reflects their level of ability to cope with conditions associated with deep water, including light, oxygen, and nutrient availability.

Species can be placed into one of three ecological groups, based on their water depth tolerances and optimal water depth range: lower marsh, upper marsh, and drawdown species (Shay & Shay, 1986; Squires & van der Valk, 1992; van der Valk & Davis, 1978; Walker, 1965). Lower marsh species grow in deeper areas that are usually permanently flooded, whereas upper marsh species grow in shallower areas that are only seasonally flooded. Drawdown species can grow in a range of water depths, but are highly influenced by hydroperiod; they have a life span of only several years under sustained water levels (Squires & van der Valk, 1992).

Lower marsh species such as the hybrid cattail (*Typha x glauca*) and softstem bulrush (*Schoenoplectus tabernaemontani*, syn. *Scirpus lacustris* spp. *glaucus*) generally increase their aboveground biomass in deeper water (Squires & van der Valk, [1992](#); Waters & Shay, [1990](#)). They will, however, exhibit reduced biomass as water depth reaches and exceeds their known water depth range (Squires & van der Valk, [1992](#)). Bedish ([1967](#)) found that the hybrid cattail experienced reduced growth in sites with no standing water and concluded this reflects its high moisture requirement.

Upper marsh species such as wheat sedge (*Carex atherodes*), common reed (*Phragmites australis*), and whitetop grass (*Scolochloa festucacea*) exhibit similar patterns in biomass as lower marsh species, but over a shallower water depth range (Squires & van der Valk, [1992](#)).

Drawdown species intolerant of deep water, such as saltmarsh bulrush (*Bolboschoenus maritimus*, syn. *Scirpus maritimus*), exhibit reduced biomass in deeper water (Lieffers & Shay, [1981](#); Squires & van der Valk, [1992](#)).

Hydroperiod

Flood and drought episodes, or lack thereof, can influence growth performance and nutrient content. In an experimental prairie marsh flood event, biomass of white sedge (*Carex atherodes*), whitetop grass (*Scolochloa festucacea*), common reed (*Phragmites australis*), softstem bulrush (*Schoenoplectus tabernaemontani*, syn. *Scirpus lacustris* spp. *glaucus*) and hybrid cattail (*Typha x glauca*) declined significantly in the first year of flood (van der Valk, [1994](#)). In a separate experiment, van der Valk & Davis ([1980](#)) found that drawdown reversed the decline in biomass of softstem bulrush (*Schoenoplectus*

tabernaemontani, syn. *Scirpus validus*), which had begun to decline several years after the previous drawdown. In contrast, broad-fruited burreed (*Sparganium eurycarpum*) biomass declined during the drawdown, while the hybrid cattail (*Typha x glauca*) biomass was unaffected during drawdown but declined the following year during reflow. Boers & Zedler (2008) found that stabilized water levels increased P accumulation and growth of the hybrid cattail (*Typha x glauca*).

Sediment Chemistry

Sediment oxygen levels and redox potential influence nutrient availability for plant uptake (Bowden, 1987; Dunne & Reddy, 2005). In general, decreasing oxygen levels and redox potential make N less available and P more available (Bowden, 1987; Dunne & Reddy, 2005). These conditions are typical of deeper water in prairie marshes. Nutrient availability can affect both emergent macrophyte growth performance and nutrient content (Boers & Zedler, 2008; Boyd & Hess, 1970; Grace, 1988; Li et al., 2010; Lorenzen et al., 2001; Neill, 1990).

Increasing nutrient availability may enhance emergent macrophyte growth performance. Lorenzen et al. (2001) found that southern cattail (*Typha domingensis*) produced more leaves in low oxygen conditions and when high levels of P was added. Southern cattail also exhibited increased growth performance with P addition but reduced growth in low redox potential sediments (Li et al., 2010). Increased P availability to hybrid cattail (*Typha x glauca*) results in increased biomass (Boers & Zedler, 2008; Grace, 1988). Neill (1990) found that hybrid cattail and whitetop grass (*Scolochloa festucacea*) growth increased with N addition.

It has been reported that emergent macrophyte nutrient content increases with increased nutrient availability (Boyd & Hess, 1970). Boers & Zedler (2008) found that addition of P increased hybrid cattail tissue P concentration. Southern cattail N and P concentrations increased under increased P availability and in sediments with high redox potential (Li et al., 2010).

1.3.4. Species Zonation

Prairie marsh emergent zones often exhibit distinct concentric bands of plant species or assemblages surrounding the deepest part of the marsh that progress outward along the water-depth gradient (Kantrud, et al., 1989; Stewart & Kantrud, 1971). These zones are created when environmental factors vary along a horizontal and/or vertical plane, which separates species along the gradient based on their tolerance of the changing conditions, creating a coenocline (Spence, 1982). Horizontal factors include sediment type and wave or wind turbulence (Spence, 1982). Vertical factors include water depth and permanence, light availability, temperature, salinity, water density, pressure, and turbulent motion (Grace, 1989; Spence, 1982; Squires & van der Valk, 1992; Stewart & Kantrud, 1971). Water depth and light availability are perhaps the most important factors in prairie marsh zonation, especially where water levels are stable (Squires & van der Valk, 1992).

Tolerance to an environmental variable is largely determined by emergent macrophyte morphology and physiology (Squires & van der Valk, 1992). For example, the large rhizomes of *Typha angustifolia* enable it to support its tall narrow leaves in deep water, whereas the smaller rhizomes of *T. latifolia* restrict it to shallower water (Grace & Wetzel, 1982). The degree to which an emergent macrophyte species is capable of oxygenating its rhizosphere will determine the level of hypoxia and depth of water it can

tolerate (Spence, [1982](#)). Wießner et al. ([2002](#)) found that *Typha latifolia* was better able to oxygenate its rhizosphere than *Phragmites australis* under the same sediment conditions.

Zonation may also result from interspecific competition. Grace & Wetzel ([1982](#)) found that *Typha angustifolia* occupied a wide range in water depth in the absence of *T. latifolia*, but was competitively displaced to deeper water in its presence.

1.3.5. A Prairie Marsh Invasive: Hybrid Cattail (*Typha x glauca*)

Sympatric hybridization of the North America native broad-leaf cattail (*Typha latifolia*) and invasive narrow-leaf cattail (*T. angustifolia*) results in a F₁ hybrid cattail (*T. x glauca*) (Boers et al., [2007](#)). Hybrid cattails are found in regions of northeastern and central North America (Kuehn & White, [1999](#)). Its presence in North America dates as early as the 1940s (Smith, [1967](#)) (Figure 2). The hybrid cattail is probably widespread across the Canadian Prairies; Wasko ([2013](#)) sampled 39 wetland sites in southern Manitoba and southeastern Saskatchewan, including Oak Hammock Marsh and Delta Marsh, Manitoba, and found 18 contained only *T. x glauca* and eleven had at least 50% *T. x glauca* cover with the remaining cover comprised of *T. latifolia*.

While *T. latifolia* and *T. angustifolia* can be identified using easily-measured gross external morphological characters such as leaf length and thickness, rhizome size, pistillate and staminate spike width, and distance between spikes (Grace & Wetzel, [1981](#)) (Figure 2 and Figure 3), distinction of the hybrid from either parent species using these measures is near impossible. Kuehn & White ([1999](#)) found that external morphology characters of the hybrid are highly variable and intermediate between but often overlap

with parent species, thus making identification of the hybrid subjective. Alternative identification methods include pollen characters (Finkelstein, [2003](#)), internal leaf cellular structures (McManus et al., [2002](#); Wasko, [2013](#)) (Figure 4), protein assays (Krattinger et al., [1979](#)), and genetic analyses (Kuehn & White, [1999](#)). However, each of these methods presents its own limitations, such as restricted sampling opportunities for pollen, as well as time, cost, and expertise required to conduct the analyses.

The hybrid tolerates a wider range of water depths than either parent species. In general, *T. latifolia* is found in sites 15 cm above water level to 80 cm of standing water, while *T. angustifolia* is found in standing water from 50 cm to 100 cm (Grace & Wetzel, [1981](#)). Hybrid cattail can occupy moist soil to sites with standing water deeper than 100 cm (Boers et al., [2007](#)). It is also able to grow under wide ranges in a variety of environmental variables (Kuehn & White, [1999](#)). Waters & Shay ([1990](#), [1992](#)) studied morphological characters along a water depth gradient and concluded that morphological plasticity of the hybrid cattail is a major contributing factor to its high tolerance of prevailing environmental conditions and ability to grow under a wide range of conditions which they considered highly advantageous for a hybrid that relies on vegetative reproduction.

The hybrid cattail is capable of expanding rapidly through vegetative reproduction (Boers et al., [2007](#)). Waters & Shay ([1990](#)) concluded that the hybrid cattail inherited the vigorous vegetative habit of *T. latifolia* and the deep water tolerance of *T. angustifolia*. The result is a highly invasive cattail more aggressive than either parent species (Boers et al., [2007](#)).

Increased hybrid cattail growth and reduced emergent macrophyte species diversity have been documented following wetland disturbances such as water level stabilization, sustained flooding, increased nutrient input, and increased sediment loading (Boers et al., [2007](#); Boers & Zedler, [2008](#); Kuehn & White, [1999](#); Woo & Zedler, [2002](#)). Under these conditions, *T. x glauca* becomes competitively superior and supersedes native species through aggressive vegetative growth, often forming large monodominant stands (Boers, [2007](#); Boers & Zedler, [2008](#)). Monodominant stands can result in reduced use by wetland birds because they do not provide the necessary habitat heterogeneity (Kantrud, [1986](#); van der Valk & Davis, [1980](#)). Prairie marshes are increasingly subject to such disturbances that favour hybrid cattail dominance at the expense of emergent macrophyte diversity.



Figure 2. Provincial biologist holding shoots of the North America native broad-leaf cattail (*Typha latifolia*) on the left, and invasive narrow-leaf cattail (*T. angustifolia*) on the right, collected from Delta Marsh, Canada, in July 1949 (photo © G. F. Bondar, reprinted from McLeod et al., [1949](#)).

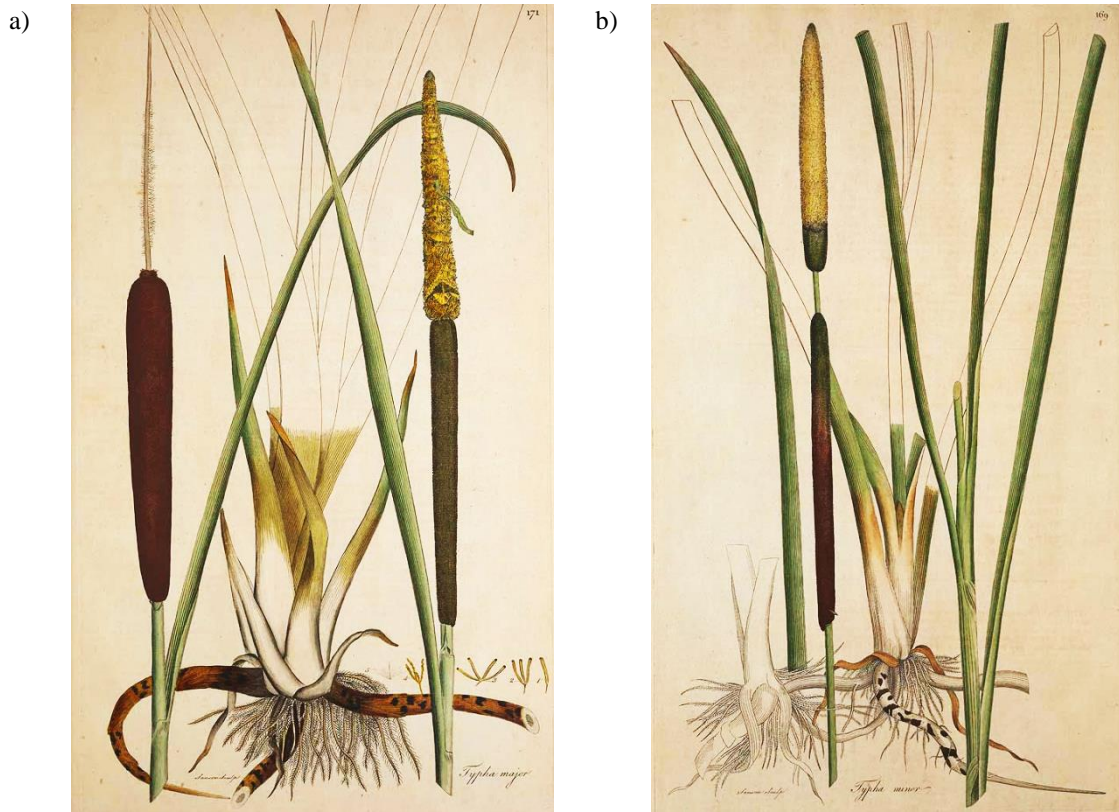


Figure 3. Botanical drawings of (a) broad-leaf cattail (*Typha latifolia*, historically called *Typha major*) and (b) narrow-leaf cattail (*Typha angustifolia*, historically called *Typha minor*) demonstrating morphological differences in diameter of pistillate spikes, distance between pistillate and staminate spikes, and leaf width (reprinted from Curtis, 1798).

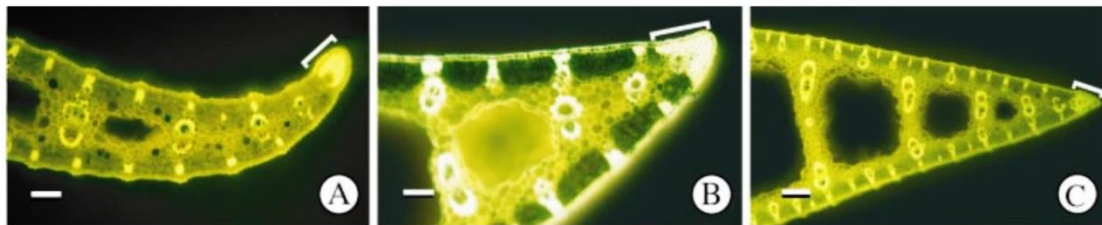


Figure 4. Leaf cross sections of (a) broad-leaf cattail (*Typha latifolia*), (b) narrow-leaf cattail (*T. angustifolia*), and (c) hybrid cattail (*T. glauca*) demonstrating differences in leaf shape and anatomy (modified from McManus et al., 2002).

1.4. Prairie Marsh Wet-Dry Cycle

Prairie marshes experience a cyclical change in vegetation (Harris & Marshall, 1963; van der Valk & Davis, 1978). This cycle is often called the wet-dry cycle because the change in vegetation is largely driven by alternating flood and drought years (Kantrud, 1986; Shay & Shay, 1986). The cycle may take anywhere from 5 to 30 years to complete (van der Valk & Davis, 1978); areas that experience moderate precipitation and temperature generally exhibit the fastest cycle completion (Johnson et al., 2005). Changes in vegetation influence the entire marsh ecosystem, including its sediment and water conditions, fauna, and other flora (van der Valk & Davis, 1978). Using data combined from literature, van der Valk & Davis (1978) developed a model of the prairie marsh wet-dry cycle, with stages that reflect changes in vegetation abundance and dominance (Figure 5). The wet-dry cycle consists of five marsh stages: dry marsh, regenerating marsh, hemi-marsh, degenerating marsh, and lake marsh (Figure 6).

Different stages of the wet-dry cycle may be more or less desirable for managers of hydrologically controlled prairie marshes depending on the purpose of management, such as habitat restoration versus nutrient removal. No one stage is likely to meet all management goals. However, managing an altered marsh so that it progresses from one stage to the next and continues to follow the wet-dry cycle is desirable if returning the marsh to its natural state is the main management goal.

Dry Marsh Stage

Prairie marsh bottoms may become partially or fully exposed mudflats in years when precipitation is sufficiently below normal to cause drought (Figure 5, Figure 6). Artificial

drawdown in managed wetlands can achieve similar conditions. Regardless of cause, drawdown has one major result: rapid germination of mudflat and wetland plant species from seeds in the marsh soil seed bank (Kadlec, 1962; van der Valk & Davis, 1978).

In their study of prairie marsh seed banks, van der Valk & Davis (1978) found that seeds from perennial emergent macrophytes could germinate on exposed mudflats or in very shallow water, while seeds from annual mudflat species germinated on exposed mudflats only. They concluded that successful germination and seedling growth of emergent macrophyte and annual mudflat species can occur only during drawdown.

Annual mudflat species establish and mature quickly in the dry marsh stage; they produce seeds by the end of summer. These replenish the seed bank, but also provide food for many bird species, in addition to seeds from the exposed seed bank (Kadlec, 1962). Emergent macrophytes do not typically flower in their first year of growth (van der Valk & Davis, 1978). Exposed shorelines and mudflats of the dry marsh stage provide suitable habitat for shorebirds (Kantrud, 1986).

Drawdown exposes marsh soils to oxygen, enabling processes that are inhibited by the anaerobic conditions of flooded water, such as decomposition of organic matter, which improves soil condition (Kadlec, 1962; Kantrud, 1986). The dry marsh stage ends with the return of normal water levels (van der Valk & Davis, 1978).

Regenerating Marsh Stage

When prairie marshes are reflooded, either artificially or from the return of normal rainfall, annual mudflat species stop germinating and the mature plants are eliminated (van der Valk & Davis, 1978). Emergent macrophytes cease germinating in all but the

shallowest of areas, but continue to grow and increase in abundance through vegetative reproduction, as well as produce vast quantities of seed (van der Valk & Davis, 1978). Seeds from submerged and free-floating macrophyte germinate under the reflooded conditions, allowing these plants to reestablish in deeper areas. The overall appearance of the regenerating marsh stage is that of a rejuvenating marsh (Figure 5, Figure 6).

Hemi-Marsh Stage

The hemi-marsh stage is perhaps the most diverse and productive. It exists when there are approximately equal amounts of emergent macrophyte cover and open water, which are interspersed to create a heterogeneous landscape (Murkin et al., 1997) (Figure 6). During the hemi-marsh stage, a wide variety of macrophyte species are present, and in various stages of maturity. This offers better food and habitat resources than other stages, and for a wider variety of animals (Kantrud, 1986). For example, red-winged blackbirds nest in shallow marsh areas with dense vegetation, whereas yellow-headed blackbirds prefer shallow marsh areas with mixtures of open water and emergent vegetation (Murkin et al., 1997). Dabbling ducks nest and forage in areas of intermittent emergent vegetation or flooded short emergent macrophytes (Kantrud, 1986; Murkin et al., 1997). Diving ducks require areas of open water, though some prefer hemi-marsh conditions (Kantrud, 1986; Murkin et al., 1997). Any remaining exposed shorelines or mudflats can be occupied by shorebirds (Kantrud, 1986). This stage is desirable where marsh management goals include maximizing floral and faunal biodiversity.

Degenerating Marsh Stage

Prairie marshes enter the degenerating marsh stage when emergent macrophyte cover begins to decline, giving way to a larger area of open water than vegetation cover (van

der Valk & Davis, [1978](#)) (Figure 5, Figure 6). Prolonged deep water eliminates emergent macrophytes by reducing the amount of aerial tissue, and consequently the amount of oxygen transported to rhizomes and roots, which eventually leads to death of belowground tissue and prevents vegetative expansion and shoot regeneration (Ball, [1990](#); van der Valk, [1994](#)). Decline in biomass is most notable in deeper areas of the marsh where depth exceeds the tolerances of emergent macrophytes (Squires & van der Valk, [1992](#)) and exhaustion of nutrient resources is most pronounced (Coops et al., [1996](#)).

Species less tolerant of deep water, such as *Schoenoplectus tabernaemontani* (syn. *Scirpus lacustris* spp. *validus*), are often the first to disappear. Some emergent macrophyte species respond by migrating to shallower water (van der Valk, [1994](#)). Degeneration is exacerbated by intense wave action (Harris & Marshall, [1963](#)) or if water levels increase, such as during a flood event (van der Valk, [1994](#)). Submerged macrophytes remain abundant (van der Valk & Davis, [1978](#)). The resulting marsh provides habitat ideal for diving ducks (Kantrud, [1986](#)).

Deep water is not the only cause for emergent macrophyte loss; disease, insect infestations, muskrat “eat-outs”, and senescence of species with finite lifespans, such as whitetop grass (*Scolochloa festucacea*), all reduce emergent macrophyte productivity (van der Valk & Davis, [1978](#)). Because conditions are not suitable for seed germination and loss of cover can occur rapidly, emergent macrophytes are unable to maintain their productivity. As long as water levels are maintained, emergent macrophyte cover will continue to decline, especially in areas where water depth exceeds the tolerance of species present (Kadlec, [1962](#)). This stage is undesirable where marshes are managed for

nutrient removal because uptake of nutrients by plants is drastically reduced as germination and seedling growth cannot occur and vegetative spread is inhibited, and release of nutrients from leaf litter back into the aquatic system may occur.

Lake Marsh Stage

The final stage in the prairie marsh wet-dry cycle is the lake marsh, so named because the marsh resembles a large open pond or lake, with only a fringe of emergent macrophytes in shallow water around its periphery (van der Valk & Davis, [1978](#)) (Figure 5, Figure 6). Much of the remaining vegetation is eliminated by muskrat activity. Open areas are dominated by submerged and floating macrophytes, though they may not be very abundant (van der Valk & Davis, [1978](#)). Prairie marshes will remain in the lake marsh stage until the next drawdown returns them to the dry marsh stage.

Water Level Stabilization

Prairie marshes progress through the wet-dry cycle until the lake marsh stage is reached, where they will remain until natural drought or artificial drawdown returns them to the dry marsh stage. When water levels are stabilized and drawdown prevented, competitively superior emergent macrophytes like the hybrid cattail (*Typha x glauca*), form monodominant stands (Boers et al., [2007](#); Boers & Zedler, [2008](#)). Reduced emergent macrophyte diversity results in reduced habitat heterogeneity and use by wetland birds (Kantrud, [1986](#); van der Valk & Davis, [1980](#)). Periodic drawdowns can help restore biodiversity of wetland flora and fauna, and allow numerous emergent macrophyte species to exist in polydominant stands (van der Valk & Davis, [1980](#)). Engelhardt & Ritchie ([2001](#)) found high macrophyte diversity enhanced wetland

ecosystem functions and theorized a diverse wetland could support a greater abundance of fish and other wildlife.

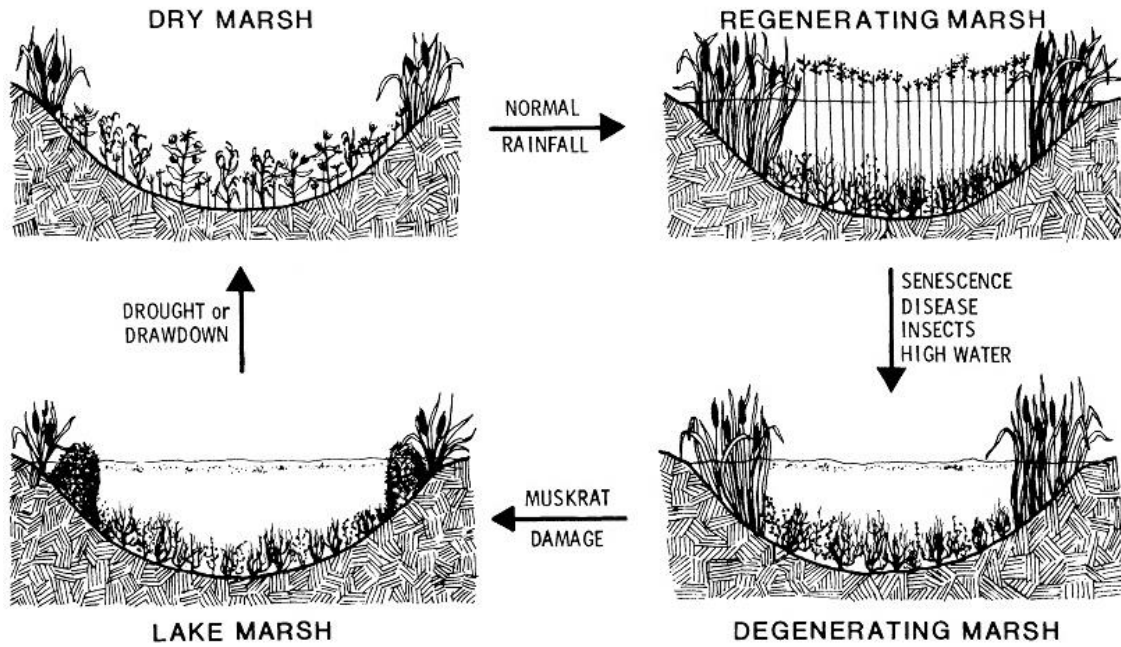


Figure 5. Changes in vegetation in a typical prairie marsh wet-dry cycle (modified from van der Valk & Davis, 1978).

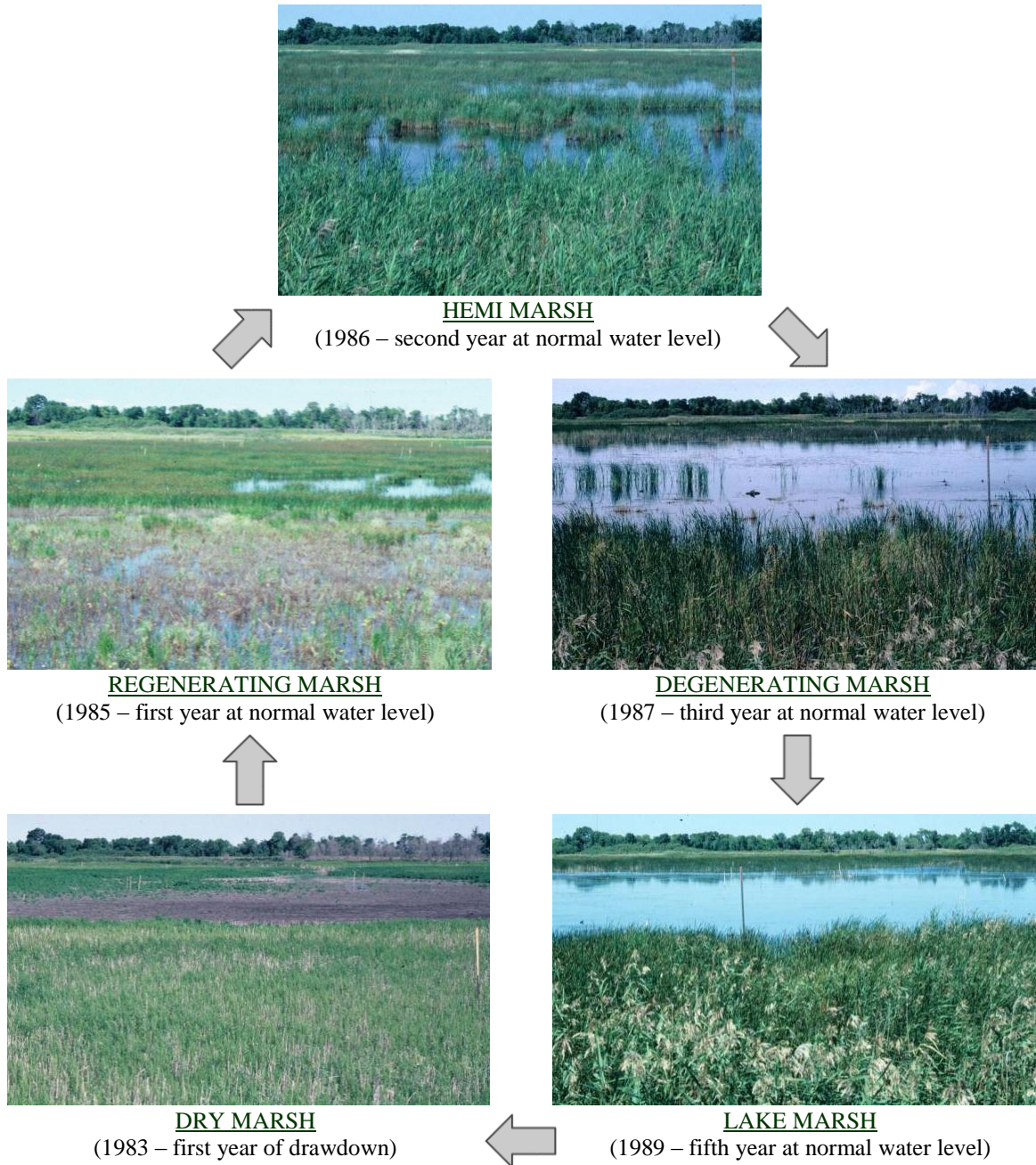


Figure 6. Changes in emergent macrophyte cover during the five stages of the prairie marsh wet-dry cycle in a Marsh Ecology Research Program experimental wetland, Delta Marsh, Canada (all images © Ducks Unlimited Canada).

1.5. Wetland Functions and Values

1.5.1. Ecological Benefits

Wetlands provide habitat and food to hundreds of plant and animal species (Batt, [2000](#); Boers et al., [2007](#); Fink & Mitsch, [2007](#); Johnson et al., [2005](#); Tiner, [1984](#)), including many species-at-risk in Canada such as the King Rail (*Rallus elegans*) and Swamp Rose-mallow (*Hibiscus moscheutos*) (COSEWIC, [2012](#)).

Numerous fish species use lacustrine wetlands for spawning and/or nurseries (Fink & Mitsch, [2007](#)), and feed in or upon wetland-produced food (Tiner, [1984](#)). Estuarine and coastal wetlands provide habitat for shellfish (Tiner, [1984](#)). A variety of amphibians, reptiles, and turtles require wetlands during their life (Boers et al., [2007](#); Tiner, [1984](#)), including the endangered spotted turtle (*Clemmys guttata*) (COSEWIC, [2012](#)).

Muskrats (*Ondatra zibethicus*), northern river otter (*Lutra canadensis*), American beaver (*Castor canadensis*), mink (*Mustela vison*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), weasels (*Mustela* spp.), and white-tailed deer (*Odocoileus virginianus*) benefit from the habitat and food provided by prairie marshes (Batt, [2000](#)). Fens provide habitat for endangered woodland caribou (*Rangifer tarandus caribou*) (COSEWIC, [2012](#)).

Prairie marshes provide the single most productive habitat for waterfowl in the world (Johnson et al., [2005](#)). Some bird species use wetlands year-round while migratory species, such as the endangered whooping crane (*Grus americana*) (COSEWIC, [2012](#)), use wetlands on their migratory routes for foraging, nesting, staging, and/or overwintering (Tiner, [1984](#)).

1.5.2. Environmental Benefits

Wetlands are the interface between upland and aquatic systems; because they are hydrologically linked, water flowing from the upland must pass through the wetland before reaching the aquatic system (Dunne & Reddy, 2005). Perhaps one of the most studied environmental services of wetlands is their ability to improve water quality by filtering and sequestering sediment, nutrients, metals, and other contaminants from the waters flowing through them (Anderson et al., 2013; Bowden, 1987; Boyd, 1970b; Engelhardt & Ritchie, 2001; Fink & Mitsch 2007; Johnston 1991; Matamoros et al. 2007; Tiner, 1984; Yang et al., 2008).

Suspended sediment retention improves quality of downstream water bodies by reducing turbidity and preventing adsorbed chemicals from entering them (Engelhardt & Ritchie, 2001; Tiner, 1984). Removal of excess nutrients can mitigate eutrophication (Tiner, 1984). Wetland macrophytes are an essential component of these services as they are highly productive and accumulate nutrients and other pollutants in their biomass as they grow, and have root systems that prevent erosion by stabilizing the sediment surface (Boyd, 1970b; Brix, 1994; Davis, 1991).

Wetlands are one of the most productive ecosystems in the world, and an important carbon sink and oxygen source (Environment Canada, 1991; Euliss et al., 2006; Tiner, 1984; Yang et al., 2008). Evapotranspiration from wetlands makes them microclimate regulators (Environment Canada, 1991; Tiner, 1984). Wetlands play an important role in groundwater recharge and mitigation of flood damage, especially where flood water storage capacity is high and water release is slow (Environment Canada, 1991; Fink & Mitsch, 2007; Yang et al., 2008). Emergent macrophytes in coastal and lacustrine

wetlands stabilize the shore and protect it from wind and wave action (Environment Canada, 1991).

1.5.3. Economic and Sociocultural Benefits

Wetlands are a major component of global natural capital. Olewiler (2004) defines natural capital as the beneficial services provided by the natural landscape. Services include stocks of renewable and nonrenewable natural resources, ecosystem and environmental capital, and land used for human activities (Olewiler; 2004). Ecosystem and environmental capital consists of ecological goods and services, which are extractable organisms or products and positive aspects provided by ecosystems, respectively (Burger et al., 2008).

Wetlands have social, cultural, and economic value (Gren et al., 1994; Olewiler, 2004; Tiner, 1984). Farber et al. (2002) define ecosystem value as any contribution of goods and/or services toward user-specified goals, objectives, or conditions. Value is therefore very subjective and not limited to economic profit. Despite many efforts to do so, assigning monetary value to an entire wetland ecosystem is not possible; only select services can be economically valued (Gren et al., 1994). Monetary value can be through direct profit or savings derived from wetland services.

Wetlands have direct monetary value through their provision of harvestable goods. Peat harvested from fens and bogs is used for fuel or horticultural and agricultural applications (Bowden, 1987; Environment Canada, 1991; Tiner, 1984). Timber can be harvested from swamps (Environment Canada, 1991; Tiner, 1984). Recreational fishes, such as northern pike (*Esoc lucius*), yellow perch (*Perca flavescens*), and smallmouth bass (*Micropterus*

dolomieu), spawn in deep water zones of lacustrine wetlands (Tiner, [1984](#)). Many recreationally hunted and trapped species reside in or use prairie marshes, including muskrats (*Ondatra zibethicus*), mink (*Mustela vison*), and white-tailed deer (*Odocoileus virginianus*) (Environment Canada, [1991](#); Tiner, [1984](#)). Estuarine wetlands may support large populations of palatable shellfish (Tiner, [1984](#)). Some livestock graze on upper marsh macrophyte species, such as common reed (*Phragmites australis*) and whitetop grass (*Scolochloa festacea*) (Tiner, [1984](#)).

Non-consumptive activities in wetlands like hiking, bird watching, photography, boating, and ice-skating give wetlands social, cultural, and potential economic value through ecotourism, educational programs, and research (Engelhardt & Ritchie, [2001](#); Environment Canada, [1991](#); Tiner, [1984](#)). For example, many recreational fish species spawn in deep water zones of marshes (Tiner, [1984](#)) and it has been estimated that \$24-37 billion is spent per year in the US on recreational fishing (Millennium Ecosystem Assessment, [2005](#)).

Other wetland services do not necessarily generate revenue but, if functioning properly, can alleviate expenditure. For example, storage and slow release of flood waters by wetlands can mitigate damage to flood plain developments (Tiner, [1984](#)). Coastal wetlands such as mangroves, protect the shoreline from wind and wave erosion, while delta wetlands reduce velocity of flowing water to prevent erosion (Millennium Ecosystem Assessment, [2005](#); Tiner, [1984](#)). Sequestration of nutrients in wetlands located upstream of economically important water bodies reduces the risk of damaging eutrophication.

1.6. Wetland Loss, Restoration, and Management

1.6.1. Wetland Loss

Extent of Wetland Loss

An accurate assessment of global wetland loss and degradation is made difficult by poor inventory (Millennium Ecosystem Assessment, 2005). There has been substantial wetland loss in Canada in the past century. According to Environment Canada (1991), 65% of Atlantic coastal salt marshes, 68% of southern Ontario wetlands, more than 50% of prairie potholes in Manitoba, Saskatchewan, and Alberta, 70% of Pacific estuary marshes, and 80-98% of wetlands within or adjacent to urban centres have been degraded or lost completely. Over 50% of wetlands in the continental US have been lost (Tiner, 1984). Globally, 35% of mangroves and 40% of coral reefs have been lost or degraded (Millennium Ecosystem Assessment, 2005).

Causes of Wetland Loss

Reasons for wetland loss are many, but the two primary causes are population growth and economic development (Millennium Ecosystem Assessment, 2005). Inland wetlands are often drained and/or infilled to make room for expanding urban centres, industrial areas, and agriculture (Environment Canada, 1991; Millennium Ecosystem Assessment, 2005). Coastal wetlands, such as mangroves, are converted for aquaculture (Millennium Ecosystem Assessment, 2005). Fens and bogs are drained to harvest peat, while swamps are drained to harvest timber (Environment Canada, 1991; Tiner, 1984). Wetlands in tropical and subtropical regions may be drained entirely to reduce mosquito populations and the risk of malaria, or into lake systems to reduce water loss through evaporation (Hambright & Zohary, 1998).

Intentional drainage or conversion are not the only causes of wetland loss and degradation. Overharvesting, overexploitation, and general misuse of wetlands can lead to severe degradation and loss of function. Riparian wetlands are often dredged to channelize rivers for navigation, while coastal wetlands are dredged and converted for housing developments (Tiner, [1984](#)). Coral reefs are overexploited and subject to destructive fishing practices (Millennium Ecosystem Assessment, [2005](#)). Overharvest of timber from mangroves and swamps can lead to severe degradation (Millennium Ecosystem Assessment, [2005](#)). Excessive recreational activity, such as power-boating and fishing, can damage wetlands (Environment Canada, [1991](#)). Shallow prairie potholes can become often over-grazed by cattle, or have their vegetation harvested for hay (Kantrud, [1986](#)). Suppression of prairie fires allowed excessive leaf litter to accumulate, while controlled burns in fall removed standing dead necessary for rhizome oxygenation and shoot growth in spring (Kantrud, [1986](#)).

Development and activities in areas surrounding a wetland may alter its hydrology and biogeochemistry, and consequently its health. Water control structures, such as those used for flood control and hydroelectricity production, can impact the hydrology and sedimentation of wetlands located both upstream and downstream (Environment Canada, [1991](#); Tiner, [1984](#)). Lake water level management alters coastal and prairie lacustrine marsh hydrology (Environment Canada, [1991](#)). Drainage ditches and raised highways in rural settings change water flow routes and wetland water sources (Tiner, [1984](#)). Hydrology of prairie marshes located in cropland can be drastically altered by irrigation practices (Dunne & Reddy, [2005](#); Kantrud, [1986](#)). Extraction of groundwater, oil, and gas cause subsidence of wetland bottoms (Tiner, [1984](#)).

Changes to its biogeochemistry can also degrade a wetland. Discharge of pesticides, herbicides, nutrients, and other pollutants from agriculture runoff, industrial wastewater, and domestic sewage can drastically alter wetland water and sediment chemistry (Dunne & Reddy, [2005](#); Kantrud, [1986](#); Millennium Ecosystem Assessment, [2005](#); Tiner, [1984](#)). Diversion of freshwater into estuarine wetlands can cause degradation, as can siltation of coral reefs (Millennium Ecosystem Assessment, [2005](#)). Introduction of non-indigenous species, such as reed canary grass (*Phalaris arundinacea*) and narrow-leaf cattail (*Typha angustifolia*) into prairie marshes (Aronson & Galatowitsch, [2008](#)), can drastically affect wetland ecosystem functioning (Millennium Ecosystem Assessment, [2005](#)).

Impacts of Wetland Loss

Services and values provided by wetlands are no longer available when a wetland is lost or degraded to the point where its ecosystem cannot function properly. Some of the consequences include increased shoreline erosion after riparian and coastal wetland dredging, exacerbated flood damage where flood plain wetlands were infilled, declining populations of recreationally and economically important flora and fauna that require wetland habitat, loss of harvestable wetland goods, and reduced or lost opportunity for revenue from ecotourism and educational programs.

Reduced water quality is perhaps the most prominent effect of wetland loss. Sediment, nutrients, and other pollutants flow unfiltered from upland areas into aquatic systems in the absence of healthy wetlands, which normally act as a filtering interface between the two systems (Dunne & Reddy, [2005](#)). This is a particular concern in agriculture areas where surface-applied pesticides, herbicides, and fertilizer are easily washed into adjoining streams during flood events (Young & Ross, [2001](#)). Algal blooms may increase

in occurrence and duration as a result of eutrophication (Ducks Unlimited Canada, 2008). Aquatic vegetation abundance may decline because of increased turbidity from sedimentation. Ultimately, services and values provided by the aquatic systems will be negatively impacted by wetland loss.

Sequestered nutrients, pollutants, and greenhouse gases are released and global carbon storage capacity is decreased when wetlands are drained (Ducks Unlimited Canada, 2008).

1.6.2. Wetland Restoration and Management

Protection, restoration, and construction of wetlands has increased over the last few decades in response to the negative consequences of wetland loss and in recognition of the services they provide. Restoration of drained wetlands or conversion of upland to wetlands is often conducted to restore lost habitat and regain lost services (Zedler, 2000). These wetlands may also offset negative impacts to water quality caused by their loss (Dunne & Reddy, 2005).

The ability of a wetland to filter and sequester nutrients, chemicals, and other pollutants from water has become increasingly important as eutrophication of important water bodies has been associated with wetland loss (Cole, 1998). As a result, more than one thousand constructed / treatment wetlands have been established in North America and Europe specifically to treat wastewater (Cole, 1998). Restored or constructed wetlands can also be used to treat non-point source wastewater; Zhao et al. (2009) recommend the use of riparian wetlands for treatment of agriculture runoff. Fink & Mitsch (2007)

investigated the use of a constructed river diversion oxbow wetland for treating water and found it to be successful.

1.7. Objectives and Hypotheses

Many studies show strong supporting evidence that aquatic vegetation, particularly emergent macrophytes, are both directly and indirectly involved in nutrient and pollutant removal processes by wetlands (Boyd, [1970b](#); Brix [1994](#); Davis, [1991](#); Steward [1970](#)), and are also an integral part of the wetland ecosystem for wildlife (Brix, [1994](#)). Maintaining the health and productivity of wetland macrophytes should be a key priority for wetland managers. It is therefore necessary to understand how wetland emergent macrophytes respond to surface water management when designing wetlands, wetland management strategies, and management of water bodies hydrologically connected to wetlands.

The main objectives of this study were twofold:

- 1) To improve our understanding of how emergent macrophyte growth performance and nutrient content responds to water depth and hydroperiod in prairie marshes.
- 2) To determine water depths and hydroperiod regimes that maximize productivity and nutrient uptake in prairie marshes.

The predictions of this study were:

- 1) The biomass and nutrient content of *Typha x glauca* will vary along a gradient of water depth in monodominant stands where its distribution is due to abiotic environmental preferences rather than interspecific competition.

- 2) Emergent macrophytes in marshes that experienced two years of drawdown will exhibit greater biomass and nutrient content than those in marshes subject to only one year, because the longer dry marsh stage will allow more seeds to germinate and provide higher nutrient content to marsh sediments through mineralization of organic matter accumulated during flooded years

CHAPTER 2 – Prairie Marshes in Southern Manitoba

2.1. Introduction

Much of southern Manitoba was once the bottom of glacial Lake Agassiz (Pattison et al., [2011](#)). When it and the Wisconsin glaciation Laurentide Ice Sheet receded 10,000 years ago, three large lakes were left behind, namely Lake Winnipeg, Lake Manitoba, and Lake Winnipegosis (Upham, [1890](#)), and thousands of depressions were scraped into the flat topography (Millett et al., [2009](#)).

Large lacustrine marsh complexes are associated with two of the postglacial lakes; Delta Marsh borders the southern shore of Lake Manitoba and Netley-Libau marsh surrounds the Red River inlet to Lake Winnipeg. Thousands of prairie pothole marshes have formed in the depressions due to accumulation of snowmelt and poor drainage and connectivity. Southern Manitoba is part of the Prairie Pothole Region.

Marsh soils in southern Manitoba are typically mineral hydric gleysols or regosols, having been formed as part of Lake Agassiz (Lindgren, [2001](#); Walker, [1965](#)). They are neutral to slightly alkaline (Walker, [1965](#)). The retreating glaciers and Lake Agassiz deposited lacustrine sands, silts, and clays across southern Manitoba (Shay & Shay, [1986](#)). Groundwater contains calcium and magnesium bicarbonate ($\text{Mg}(\text{HCO}_3)_2$) in the east or magnesium sulfate (MgSO_4) in the west where it is also slightly brackish (Shay & Shay, [1986](#)).

Southern Manitoba experiences long cold winters and short warm summers, during which it receives the larger portion of its precipitation. Evaporation typically exceeds

precipitation, and in the absence of secondary water sources, many prairie potholes will experience a moisture deficit and lose water (Shay & Shay, [1986](#)).

Hanuta ([2006](#)) estimated that wetlands covered approximately 10% of southern Manitoba in the 19th century, but now cover less than 1% of the area. Presently, much of southern Manitoba land use is agriculture. Because of the topography and climate, seasonal flooding and excess water present a problem to landowners and the agriculture industry (Pattison et al., [2011](#)). An estimated 70-80% of wetlands that existed in southern Manitoba prior to human settlement have been lost to drainage to create arable farmland and to prevent its flooding (Figure 7) (Oak Hammock Marsh, [2006](#); Pattison et al., [2011](#)).

Oak Hammock Marsh and Delta Marsh are two southern Manitoba prairie marshes of great importance. Both are major staging areas for migratory birds and function in improving water quality. Oak Hammock Marsh includes an interpretive centre that is integral to wetland education in Manitoba. Delta Marsh is one of the largest freshwater marshes in Canada and was once a hot spot for migratory waterfowl.

2.2. Oak Hammock Marsh Wildlife Management Area

Oak Hammock Marsh Wildlife Management Area (hereafter OHM) is located 50 km north of Winnipeg, Manitoba (N50°11.271, W097°07.204) and is comprised of approximately 17.2 km² of dry upland and 18.7 km² of wetland. Upland areas include waterfowl lure crops, aspen-oak forests, a willow bluff, and tall-grass prairie, while wet meadows and prairie basin marshes form the wetlands (Oak Hammock Marsh, [2006](#)). OHM also includes numerous canals and creeks, as well as a constructed wetland system

for wastewater treatment. Scattered throughout OHM are approximately 80 constructed nesting islands and 50 artificial nesting structures.

History of Oak Hammock Marsh Wildlife Management Area

The OHM marshes are restored remnants of the historical St. Andrews Bog, which stretched from Winnipeg to Teulon, in the Netley-Grassmere Watershed, Manitoba. It once covered approximately 470 km² (Figure 7), but was drained in 1896 for agriculture and urban development, reducing its size to 0.6 km² (Oak Hammock Marsh, [2006](#)). Drainage of St. Andrews Bog and its subsequent conversion to agriculture and development of rural subdivisions resulted in severe loss and degradation of wetland, riparian, forested, and aquatic habitats in the Netley-Grassmere Watershed (Water Stewardship Division, [2011](#)). Many of the services it provided were also lost, including filtration of surface water, resulting in reduced water quality in downstream water bodies.

To restore lost habitat and mitigate water quality reduction, the Manitoba provincial government began acquiring land surrounding the remnant of the St. Andrews Bog in the 1960s with financial aid from the federal government Fund for Rural Economic Development program. Manitoba Conservation and Ducks Unlimited Canada started constructing 22 km of earth dykes in 1972 and in the spring of 1973 the marshes of OHM were complete. Additional construction in 1983 divided OHM into four large and two small wetland cells which resemble linked basin marshes under the Canadian Wetland Classification System (NWWG, [1997](#)).

Oak Hammock Marsh was one of the first wetlands to be included in the Manitoba Heritage Marsh Program in 1985 (Manitoba Information Services, [1985](#)). The program is

a partnership involving the Manitoba government, Ducks Unlimited Canada, the Manitoba Wildlife Federation, and the Manitoba Naturalists Society. Heritage marshes are chosen based on their public importance due to environmental, economic, recreational, and education features, and receive long-term protection and active management from all parties involved in the program.

Oak Hammock Marsh became a “wetland of international importance” for wildlife and people under the Ramsar Convention on Wetlands in 1987 (Ramsar, [2001](#)) because of its high use as a breeding and staging area for waterfowl and migratory birds (Ramsar, [2014](#)).

Construction of the Conservation Centre, which houses Ducks Unlimited Canada national headquarters, Manitoba Conservation offices, and the Oak Hammock Marsh Interpretive Centre, was completed in 1993. The Interpretive Centre offers access to the wetlands and upland through more than 30 km of trails which are visited by more than 200,000 tourists annually (Lynch-Stewart, [2008](#)). BirdLife International designated OHM a globally significant Important Bird Area in 2001, due to its importance to congregatory birds and its high waterfowl concentrations, particularly of shorebird species (Lindgren, [2001](#); Wren & Couturier, [2009](#)).

OHM and the Agamon Hula wetland in Israel became “twin marshes” in 2010, as part of a collaboration on wetland science and management between the provincial government of Manitoba and the Keren Kayemeth Leisrael (KKL) – Jewish National Fund, with Ducks Unlimited Canada as a cooperating partner (Government of Manitoba, [2011](#)). OHM and Agamon Hula wetland have much in common: both are situated in

ecologically and economically important watersheds and trans-continental north-south bird migration flyways; they have similar histories as they are both remnants of larger wetlands that were drained and the land converted to agriculture, but later partially restored and now monitored and managed for education and tourism; and both are Important Bird Areas and Ramsar wetlands. Areas of cooperation include promotion of both wetlands through provision of public information, development and sharing of information on science activities, including monitoring and management, exchanges of wetland scientists and managers, and development of an educational curriculum for Manitoba and Israeli students to learn about OHM and the Agamon Hula.

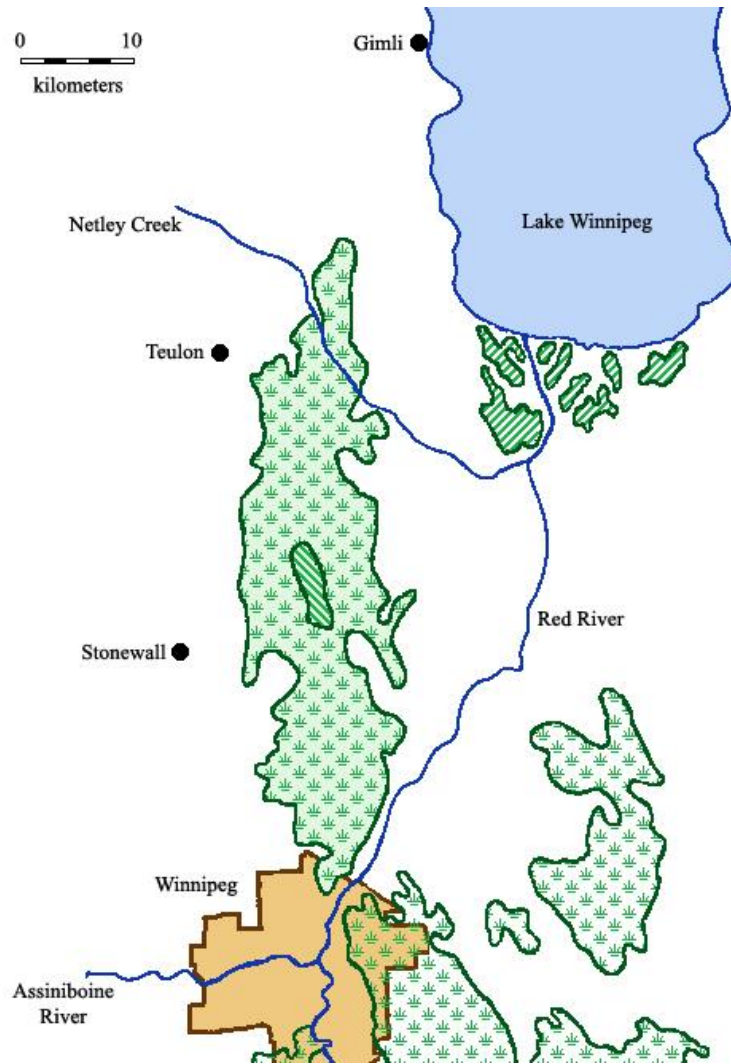


Figure 7. St. Andrews Bog (🌿), other historical wetlands (🌿), and present-day Oak Hammock Marsh (🌿) and Netley-Libau Marsh (🌿), Manitoba, Canada (modified from Nielsen et al., 1996).

Oak Hammock Marsh Wetlands

OHM has four large and two small wetland cells. The large cells, numbered 1 through 4 (see Figure 8), range from 3.6 to 5.6 km² in size and contain approximately eighty 1,400 to 2,700 m² artificial nesting islands. Adjacent to the Conservation Centre and accessible via paths and boardwalks are the two smaller cells, Teal and Coot, which are only 0.2 to

0.3 km² in size (Figure 8). Cell hydrology, geochemistry, flora, and fauna are similar to prairie basin marshes.

The nearby town of Stony Mountain experiences annual, July, and January temperatures of 3.1°C, 19.9°C, and -16.4°C, respectively. The area receives 550.1 mm of precipitation each year, of which 435.6 mm is from rainfall (Environment Canada, [2015c](#)).

Water sources for the marshes include overland flood waters from snowmelt, rain, surface runoff from agriculture, water transported via Wavey Creek, and artesian spring water. Parks Creek, Dewar Drain, and Wavey Creek drain the marshes into the Red River and ultimately Lake Winnipeg (Figure 8) (Oak Hammock Marsh, [2006](#)).

OHM marsh soils are a Red River Clay-Osborne Association of gleysols (Lindgren, [2001](#)), having been formed as part of Lake Agassiz and later St. Andrews Bog. They are calcic, slightly alkaline, and rich in organic matter.

Oak Hammock Marsh emergent vegetation is dominated by monotypic stands of cattails (*Typha* spp.), but also includes common reed (*Phragmites australis*), sedges (*Carex* spp.), bulrushes (*Schoenoplectus* spp.), and rushes (*Juncus* spp.). Wasko ([2013](#)) found that at least 50% of the *Typha* present at OHM was the hybrid cattail (*T. x glauca*) and the remainder was broad-leaf cattail (*T. latifolia*). In 1997, the wetland area of Cell 4 was mostly unvegetated (47%) or dominated by cattail (35%) (McDougal, [2001](#)). Less common are broad-fruited burreed (*Sparganium eurycarpum*), water parsnip (*Sium suave*), water hemlock (*Cicuta maculate*), arrowgrass (*Triglochin* spp.), mint (*Mentha arvensis* and *Stachys palustris*), marsh marigold (*Caltha palustris*), parnassus (*Parnassia* spp.), Northern water-plantain (*Alisma triviale*), swamp lousewort (*Pedicularis*

lanceolata), and common mare's tail (*Hippuris vulgaris*). Non-emergent wetland species found at OHM include duckweed (*Lemna* spp.), and common bladderwort (*Utricularia vulgaris*) (Lindgren, 2001; Oak Hammock Marsh, 2014).

OHM is home to a wide variety of birds; at least 296 species have been seen in the marshes and surrounding upland (Lindgren, 2001). Many species are found in numbers high enough to be considered globally and/or continentally significant, particularly during spring and fall when OHM is used as a migratory staging area. These numbers are a major contributing factor to the designation of OHM as Ramsar wetland and an Important Bird Area. Wetland-associated birds found at OHM include a variety of dabbling ducks, diving birds, shorebirds, wading birds, geese, and gulls. Pervasive throughout the marshes are muskrats (*Ondatra zibethica*) and their dens (Oak Hammock Marsh, 2014). Muskrats play an important role in transitioning OHM cells from the degenerating to lake marsh stage of the wet-dry cycle.

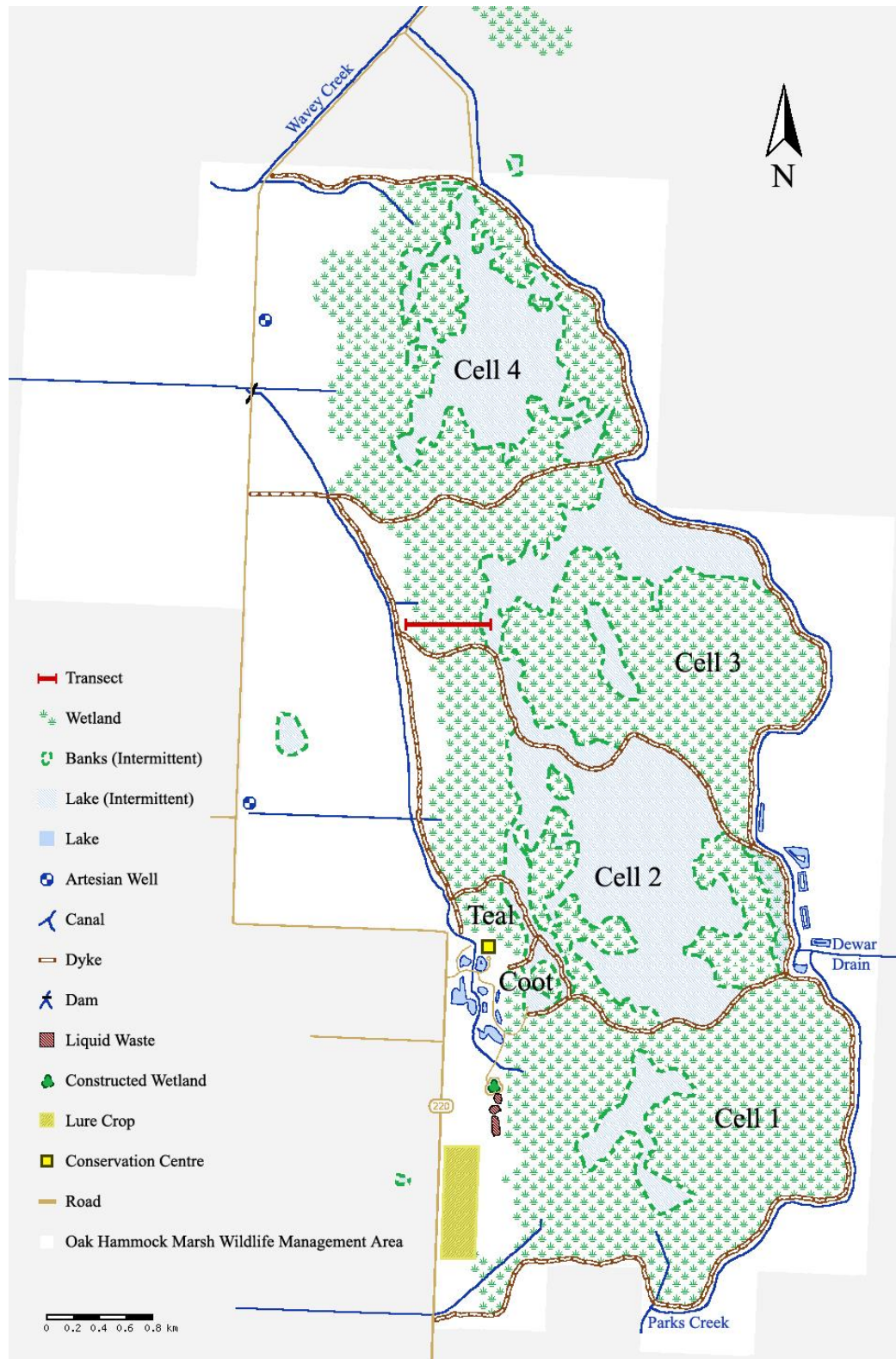


Figure 8. Oak Hammock Marsh Wildlife Management Area, Manitoba, Canada (note: wetland vegetation cover is an approximation of cover in 2012 based on Natural Resources Canada topographic maps and Google Earth imagery).

Hydroperiod Management

The OHM wetland cells are separated by earth dykes and equipped with canals and dams to facilitate water distribution and drainage (Figure 8). Water levels of each cell are managed by Manitoba Conservation to follow a drawdown and re-flood cycle that mimics natural water level fluctuations. Cells can be managed independently of each other and are usually in different stages of the cycle, to ensure a variety of habitats exist simultaneously. Drawdown of a given cell is scheduled once its appearance begins to resemble that of a lake marsh, with large areas of open water and emergent vegetation found only in fringing shallow areas (Figure 9). Cells are passively drained in spring and left dry for one or two years, depending on vegetation regrowth and germination (Oak Hammock Marsh, [2004](#)). Teal Cell was drained in 2004, followed by Cell 3 in 2007, Cell 1 in 2012, and Cell 2 in 2013 (Oak Hammock Marsh, [2004](#); R. Bruce, personal communication, July 6, 2015).



Figure 9. Change in emergent macrophyte cover over a ten-year period (2002 to 2012) of sustained water levels in Cell 2 (bottom) and before and after the one-year drawdown in 2007 of Cell 3 (top) at Oak Hammock Marsh, Manitoba (Source: Google™ Earth, ©DigitalGlobe, 2015, Image Dates 9/11/2002 and 25/9/2012).

2.3. Delta Marsh and the Marsh Ecology Research Program

2.3.1. Delta Marsh

Delta Marsh is a complex 185 km² wetland that stretches along the southern shores of Lake Manitoba from St. Ambrose to Lynch Point, Manitoba, Canada (N50°12.485, W098°13.030) (Figure 10). Approximately 166 km² of Delta Marsh is under public ownership as provincial Crown land. The remainder of the wetland is privately owned and includes agriculture land and the coastal cottage community of Delta Beach, which has fewer than 200 cottages (Brown, 2003).

Delta Marsh was recognized as a wetland of international important for wildlife and people under the Ramsar Convention on Wetlands in 1982 (Ramsar, 2001). In 1988 the province designated it a Manitoba Heritage Marsh for its environmental, economic,

recreational, and education features. It became a globally significant Important Bird Area in 1991 by BirdLife International because of its importance to congregatory waterbirds, and the size of said congregations (Wren & Couturier, [2009](#)). As of 2011, 113 km² of the public wetland is protected as a provincial Wildlife Management Area. Delta Marsh receives 50 to 5,000 visitors per year (Lynch-Stewart, [2008](#)).

Delta Marsh Wetlands

A forested sand ridge separates Delta Marsh from Lake Manitoba, thus classifying it as a lacustrine lagoon marsh under the Canadian Wetland Classification System (NWWG, [1997](#)). However, the wetland includes numerous large bays, each more than 10 km² in size with water as deep as 3 m, and many smaller bays less than 10 km² in size that typically have water less than 1 m deep (Batt, [2000](#)). Areas of true marsh formed from stands of dense vegetation are extensive throughout the wetland. Located within the stands are smaller ponds less than 0.05 km² in size with water no deeper than 50 cm (Batt, [2000](#)). Channels and creeks connect Assiniboine River to the marsh, and the marsh to Lake Manitoba.

Delta Marsh is a mineral wetland, though it has a thin layer of peat (Shay & Shay, [1986](#)). Soils are gleysols and regosols, and neutral to slightly alkaline (Walker, [1965](#)). Water is moderately brackish (Batt, [2000](#)).

Mean annual, July, and January temperatures are 2.6°C, 19.3°C, and -16.2°C, respectively (Environment Canada, [2015a](#)). Annual precipitation for the marsh is approximately 525.7 mm, with 403.9 mm as rainfall (Environment Canada, [2015a](#)).

Water sources for the marshes include snowmelt, rain, surface runoff from agriculture, and water transported by Assiniboine River collected from southwest Manitoba, southeast Saskatchewan, and northwest North Dakota. Marsh waters drain into Lake Manitoba through a number of connecting channels and breaks in the sand ridge. Fairford River at the northeast end of Lake Manitoba drains its waters into Lake Winnipeg. Because the two are connected through channels and breaks in the sand bar, Delta Marsh exhibits occasional short-term localized water level fluctuations when Lake Manitoba experiences seiche action (Batt, [2000](#)).

In 1961 the Fairford River was channelized and a dam and water control structures were built at its origin on Lake Manitoba to mitigate damage to agricultural fields, beach property, and Delta Beach during high water level years, and potential reduction in fish stock in low water level years (Batt, [2000](#)). The lake has since been managed to maintain stable water levels at 247.5 ±0.3 m AMSL (Batt, [2000](#)). Consequently, marsh water levels have been stabilized since 1961. Construction of the Fairford dam reduced the range in lake and marsh water levels from 2.1 m to 0.6 m (Shay & Shay, [1986](#)). Batt ([2000](#)) considers the Fairford dam to be a greater influence on Delta Marsh than any major geologic, climatological, or other anthropogenic intervention in the last several centuries. Delta Marsh hydrology was further altered with the construction of the Assiniboine River Floodway / Portage Diversion in 1969, which is used to divert floodwaters from Assiniboine River to the lake across the marsh (Batt, [2000](#)).

Deep marsh areas in Delta Marsh are dominated by two emergents: cattail (*Typha latifolia*, *T. angustifolia*, and *T. x glauca*) and to a lesser extent bulrush (*Schoenoplectus lacustris*) (Batt, [2000](#); Shay et al., [1999](#); Shay & Shay, [1986](#); Squires & van der Valk,

1992). Shallow marsh areas are dominated by sedges (*Carex* spp.), common reed (*Phragmites australis*), and whitetop grass (*Scolochloa festucacea*) (Squires & van der Valk, 1992). Cattail, bulrush, whitetop grass, and common reed form the largest monodominant zones in the marsh (Squires & van der Valk, 1992). The hybrid cattail, *T. x glauca*, has been present in the marsh since the 1940s.

Prior to construction of the Fairford Dam, the two most prevalent wetland plants in Delta Marsh were *Phragmites australis* and *Scolochloa festucacea*. Today the shorelines are dominated by *Typha x glauca* (Batt, 2000) and backed by small stands of *Phragmites australis* and *Scolochloa festucacea* in the wet-meadow (Shay et al., 1999). In their study of six sites widely distributed at Delta Marsh and approximating 7 km², Shay et al. (1999) found that *Typha* spp. cover increased from 30% to 60% while *Phragmites* decreased from 43% to 17% following construction of the dam. Water level stabilization may explain the shift in dominance, as stabilized water levels encourage the spread of certain emergent macrophytes like hybrid cattail (Shay et al., 1999; Shay & Shay, 1986). Shay et al. (1999) concluded that *Typha* spp would continue to increase in dominance as long as water levels were stabilized. Submerged wetland plants can be found in the open water areas, which are dominated by sago pondweed (*Potamogeton pectinatus*), but also include sheathed pondweed (*Potamogeton vaginatus*), water milfoil (*Myriophyllum exalbescens*), bladderwort (*Utricularia vulgaris*), coontail (*Ceratophyllum demersum*) (Shay & Shay, 1986).

Muskrat (*Ondatra zibethicus*) play an important role in the prairie marsh ecosystem and are common in Delta Marsh (Batt, 2000). Waterfowl and wetland-associated birds are

perhaps the most noticeable fauna; numerous species of dabbling duck, diving duck, shorebirds, wading birds, geese, and gulls can be found in Delta Marsh (Batt, [2000](#)).

2.3.2. Marsh Ecology Research Program

Background Information

Ducks Unlimited Canada and the Delta Waterfowl Foundation initiated the Marsh Ecology Research Program (MERP) in 1979 to improve understanding of prairie wetland ecology, particularly changes experienced during a typical prairie marsh wet-dry cycle (Murkin et al., [2000b](#)). The project was interdisciplinary, with seven major ecosystem components studied: hydrology, water chemistry, macrophyte productivity, macrophyte litter, algae, invertebrates, and vertebrates (Murkin et al., [2000b](#)). Objectives for each discipline and general summaries of data are provided by Murkin et al. ([2000a](#)) in *Prairie Wetland Ecology: The Contribution of the Marsh Ecology Research Program*. However, much of the data, including that of emergent macrophytes, were never fully analyzed.

Methods

MERP experiments were conducted from 1980 to 1989 approximately 11 km east of the Portage Diversion in Delta Marsh, Manitoba (N50° 12.495, W098° 12.949) (Figure 10). Earthen dykes were used to create ten adjacent 4-6 hectare prairie marsh-like wetland cells south of the sand ridge separating Delta Marsh from Lake Manitoba. Dykes were fitted with pumps and water control structures so that cell water levels could be manipulated to mimic the wet-dry cycle. Though Delta Marsh is a lacustrine lagoon marsh, MERP cell design made them functioned similarly to linked basin marshes under the Canadian Wetland Classification System (NWWG, [1997](#)).

MERP cells were active for ten years, during which their water levels went through four phases: baseline, deep flooding, drawdown, and sustained water levels (Murkin et al., [2000b](#)) (Figure 11). Baseline data was collected in the first year during which water levels were not manipulated, allowing cells time to adjust to dyke construction. Cells were then flooded 90 cm above normal for two years to establish similar conditions in all cells by bringing them to the lake marsh stage of the wet-dry cycle. This was followed by drawing down water levels 50 cm below normal for one or two years to allow reestablishment of vegetation. The last phase lasted for five years, during which all cells were reflooded and water depth held constant at one of three water levels.

There were four hydroperiod treatments that differed in duration of drawdown and depth of sustained water during the experimental years (Murkin et al., [2000b](#)) (Figure 11). Cells 2, 6, and 10 were subject to two years of drawdown and had high sustained water levels 60 cm above normal (i.e. 2-high). Cells 1, 5, and 9 were in drawdown for two years and reflooded to medium water levels 30 cm above normal (i.e. 2-medium). Cells 3 and 7 were subject to two years of drawdown followed by sustained normal water levels (i.e. 2-normal). Lastly, cells 4 and 8 were in drawdown for only one year and held constant at normal water levels (i.e. 1-normal). Two undyked areas equivalent in size to the MERP cells, located at either end of the cell complex were used as reference / control sites. Their water levels reflected those of Delta Marsh.

Long-term monitoring included: climatic factors such as temperature, precipitation, and evapotranspiration; physical environment factors such as soil and water temperature, sediment characterization, suspended solids, and bathymetry / topography; hydrologic factors such as water input and output, changes in cell volume, and groundwater

characterization; water chemistry such as nutrient content, conductivity, and pH; primary production including algae, macrophyte aboveground and belowground growth and nutrient content, and macrophyte decomposition; and secondary production including invertebrates, muskrat, and birds (Murkin et al., [2000c](#)).

A number of smaller short-term experiments were carried out during MERP, to address questions posed by the long-term monitoring. These included studies for at least sixteen graduate theses (Murkin et al., [2000a](#)).



Figure 10. Delta Marsh (a) wetland and (b) Marsh Ecology Research Project experimental wetland cells (numbered one through ten), Manitoba (Source: Google™ Earth, ©DigitalGlobe, 2015, Image Date 27/8/2013).

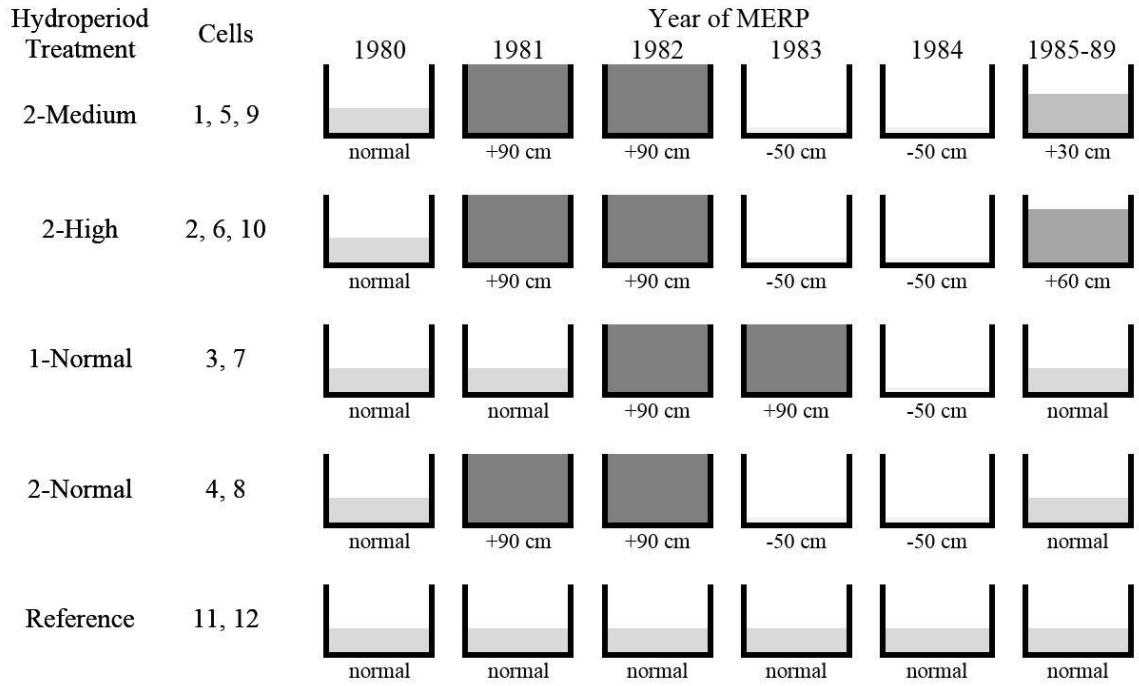


Figure 11. Marsh Ecology Research Program (MERP) cell hydroperiod treatments during baseline, deep flood and drawdown years (1980-84), and sustained water level years (1985-89) (note: water levels are given as water depth relative to normal levels (i.e. 247.5 m AMSL)).

CHAPTER 3 – Effect of Water Depth on Emergent Macrophyte Biomass and Nutrient Content at Oak Hammock Marsh, Canada

3.1. Introduction

It has long been understood that freshwater marshes can act as natural filters for nutrients, metals, and other chemicals that would otherwise flow directly into downstream water bodies (Boyd, [1970b](#); Fink & Mitsch [2007](#); Johnston [1991](#); Matamoros et al. [2007](#)). This feature of wetlands has gained international attention in recent years as nutrient-overloading, particularly of N and P, has been associated with eutrophication of many important water bodies (Cole, [1998](#)). As a result, over one thousand constructed wetlands have been established in North America and Europe to treat wastewater (Cole, [1998](#)). Many studies show strong supporting evidence that aquatic vegetation, particularly emergent macrophytes, are both directly and indirectly involved in nutrient removal (Boyd, [1970b](#); Brix, [1994](#); Davis, 1991; Steward, [1970](#)).

In addition to constructing wetlands for wastewater treatment, many wetlands are being restored from their drained state for the purpose of habitat restoration. Canada has lost 50% of its prairie potholes and 80-98% of wetlands within or adjacent to urban centres (Environment Canada, [1991](#)). Wetlands provide food and habitat to hundreds of plant and animal species (Batt, [2000](#); Boers et al., [2007](#); Fink & Mitsch, [2007](#); Johnson et al., [2005](#); Tiner, [1984](#)). A component of wetlands that is integral to the survival of wildlife, from reptiles to mammals to birds, is the diversity and health of its emergent macrophytes (Engelhardt & Ritchie [2001](#); Kantrud, [1986](#)).

From the perspective of managing wetlands, nutrient content and growth of emergent macrophytes are of particular importance, especially where constructed or restored wetlands are intended to both filter water and restore lost habitat. Successful management of wetlands therefore requires understanding how emergent macrophytes respond to environmental variables.

Many studies have looked at the effect of water depth on emergent macrophyte biomass, morphology, population parameters, and species zonation (Bedish, [1967](#); Boers & Zedler, [2008](#); Boyd & Hess, [1970](#); Coops et al. [1996](#); Grace [1988](#), [1989](#); Grace & Wetzel, [1981](#), [1982](#); Haslam, [1970](#); Lieffers & Shay [1981](#); McNaughton, [1966](#); Squires & van der Valk [1992](#); Vretare, et al., [2001](#); Waters & Shay [1990](#), [1992](#)). Others have investigated how emergent macrophyte biomass is influenced by nutrient availability, redox potential, and oxygen availability (Boyd & Hess, [1970](#); Grace, [1988](#); Li et al., [2010](#); Lorenzen et al, [2001](#); Neill, [1990](#)), which are closely linked to water depth.

In general, emergent macrophytes exhibit peak biomass over a water depth range that corresponds with optimal growing conditions for each species (Bedish, [1967](#); Squires & van der Valk, [1992](#)). Emergent macrophytes may have reduced biomass in water shallower than the optimal water depth range because of insufficient moisture (Bedish, [1967](#)), reduced P availability, as P precipitates with metallic ions under oxic conditions (Dunne & Reddy, [2005](#)), an increase in salinity beyond the tolerance of the emergent macrophyte as marsh waters evaporate (Squires & van der Valk, [1992](#)), and/or interspecific competition with species better adapted to shallow-water conditions (Grace & Wetzel; [1982](#)). Biomass in water deeper than the optimal water depth range may decline because of insufficient light for photosynthesis (Squires & van der Valk, [1992](#);

Waters & Shay, [1992](#)), insufficient oxygen for nutrient assimilation (Ambler et al., [2001](#)), reduced N availability, as denitrification is favoured under anoxic conditions while nitrification and ammonification are inhibited (Ambler et al., [2001](#)), and/or interspecific competition with species better adapted to deep-water conditions (Grace & Wetzel; [1982](#)). A common morphological response to increasing water depth exhibited by many emergent macrophytes, including *Typha latifolia*, *T. x glauca*, *Scirpus lacustris*, *S. maritimus*, and *Phragmites australis*, is an increase in shoot height (Coops et al., [1996](#); Grace, [1989](#); Grace & Wetzel, [1982](#); Haslam, [1970](#); Lieffers & Shay, [1981](#); Squires & van der Valk, [1992](#); Waters & Shay, [1990](#)). Emergent macrophyte morphology and physiology largely determines the optimal range and tolerances of water depth (Squires & van der Valk, [1992](#)).

Differences in optimal water depth ranges result in species zonation along the water depth gradient (Spence, [1982](#); Stewart & Kantrud, [1971](#)) which allows emergent macrophytes to be placed into one of three categories; lower marsh, upper marsh, and drawdown species (Shay & Shay, [1986](#); Squires & van der Valk, [1992](#); van der Valk & Davis, [1978](#); Walker, [1965](#)). Lower and upper marsh species are found in deeper permanently and shallower seasonally flooded areas, respectively. Drawdown species can tolerate a range in water depths but are eliminated by several years of sustained water levels. Squires & van der Valk ([1992](#)) investigated the distribution of seven common marsh emergent macrophytes and concluded that *Typha x glauca* and *Scirpus lacustris* spp. *glauca* are lower marsh species, *Carex atherodes*, *Phragmites australis*, and *Scolochloa festucacea* are upper marsh species, and *Bolboschoenus maritimus* and *Scirpus lacustris* spp. *validus* are drawdown species.

Fewer studies have reported on how emergent macrophyte nutrient content is affected by environmental variables such as nutrient availability, redox potential, and oxygen availability (Boyd & Hess, [1970](#); Li et al., [2010](#); Lorenzen et al., [2001](#)). Boers & Zedler ([2008](#)) studied how *T. x glauca* P uptake was affected by water level stabilization. Anderson & Mitsch ([2005](#)) investigated the effects of pulsing hydrology on nutrient uptake and found that N:P ratios, but not nutrient concentrations, were different between pulsing and steady-flow systems. Neither study investigated the effect of water depth on emergent macrophyte nutrient content.

While management has little control over wetland biogeochemical conditions, it is possible to control its hydrology, through the use of water control structures such as dams, levees and dikes, for the purpose of manipulating emergent macrophyte productivity. Inter-annual fluctuation in wetland water levels is important, but so too is managing a wetland at optimal water depths to maximize growth and nutrient content of emergent macrophytes.

Water depth changes in a wetland are not always intentional; they may be a secondary consequence of water level management for other purposes, such as lake level regulation for hydroelectric power. Water levels in lacustrine, delta, and riparian wetlands hydrologically connected to such a lake would reflect lake level management and consequently affect growth of emergent macrophytes and the services they provide. It is therefore important to understand the effects of water depth on emergent macrophyte growth to more fully understand the consequences of surface water management.

The objectives of this study were to (1) investigate how water depth affects growth performance and nutrient uptake of emergent macrophytes in a typical North America prairie marsh, and (2) determine what, if any, water depths maximized growth and/or nutrient content.

3.2. Methods

3.2.1. Study Site

This study was conducted at the Oak Hammock Marsh Wildlife Management Area, located 50 km north of Winnipeg, Manitoba (N50°11.271, W097°07.204). Oak Hammock Marsh (OHM) is a restored remnant of St. Andrews Bog. It consists of four large and two small dyked wetland cells, surrounded by upland areas (Figure 12). Water control structures allow cell water levels to be managed in order to follow a drawdown / reflood cycle meant to mimic natural water level fluctuations. Cells are drained passively once they reach the lake marsh stage of the prairie marsh wet-dry cycle, and left dry for one or two years before being reflooded. Cells are managed independently, such that multiple stages of the marsh life cycle are simultaneously represented. Teal Cell was drained in 2004, followed by Cell 3 in 2007, Cell 1 in 2012, and Cell 2 in 2013. OHM wetland cells are linked basin marshes according to the Canadian Wetland Classification System (NWWG, [1997](#)).

Very little research has been conducted in these marshes, despite OHM being a Manitoba Heritage Marsh, provincial Wildlife Management Area, Important Bird Area, and Ramsar wetland. OHM is an ideal site to study the effects of water depth because its marshes do not experience as much variation in water levels as natural marshes. Recently, Oak

Hammock Marsh and the Agamon-Hula wetland in Israel were declared “twin marshes” by Manitoba and Israel as an outcome of the Jewish Federation of Winnipeg’s 2010 mission to Israel to conduct joint research on the fate of wetlands in agriculture areas subject to hydrologic disturbance (Government of Manitoba, 2011).

Coops et al. (1996) and Squires & van der Valk (1992) concluded that at least three years of flooded conditions are necessary for emergent macrophytes to fully respond to water depth. At the time of sampling, only Cell 3 had experienced at least three years of flooded conditions but had not yet progressed into the degenerating stage of the wet-dry cycle. Therefore, samples were collected from Cell 3, which was in the sixth growing season since its drawdown in 2007 (R. Bruce, personal communication, July 6, 2015). Cells 1, 2 and 4 were unsuitable for sampling because they were in the regenerating, dry, and lake marsh stages, respectively, as described by van der Valk & Davis (1978).

OHM marsh soil is a Red River Clay-Osborne Association of gleysols (Lindgren, 2001), having been formed as part of Lake Agassiz and later St. Andrews Bog. They are calcic, slightly alkaline, and rich in organic matter. Water inputs include overland flooding from snowmelt, rain, agricultural runoff, and artesian springwater. A series of canals facilitate flooding and draining of the cells (Figure 12). The dominant emergent macrophyte is *Typha* spp., but *Schoenoplectus* spp. and *Phragmites australis* are also present. Wasko (2013) found that at least 50% of the *Typha* present at OHM was the hybrid cattail (*T. x glauca*) and the remainder was broad-leaf cattail (*T. latifolia*).

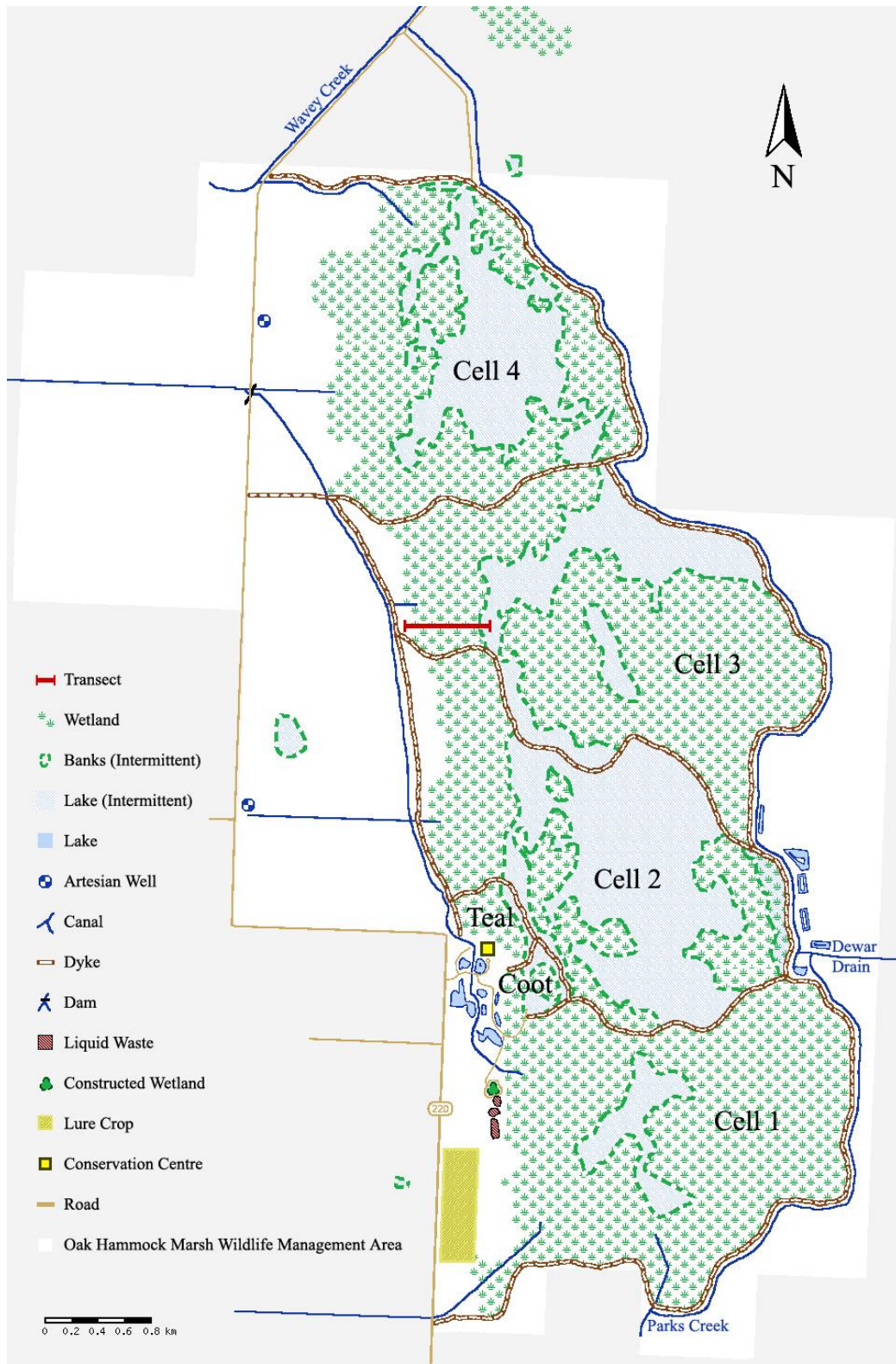


Figure 12. Oak Hammock Marsh Wildlife Management Area, Manitoba, Canada (note: wetland vegetation cover is an approximation of cover in 2012 based on Natural Resources Canada topographic maps and Google Earth imagery).

3.2.2. Field Collection and Sample Processing

Wherever possible, field sampling and laboratory analyses were designed to follow the Marsh Ecology Research Program methods as closely as possible to allow for direct comparison of results (Murkin et al., 2000c; van der Valk, 1989).

A broad survey of Oak Hammock Marsh Cell 3 revealed that its bathymetry/topography is relatively uniform, with changes in water depth no greater than 40 cm over distances less than 50 metres. However, the marsh is rife with narrow pits and bumps, possibly a result of uneven accumulation of detritus and its incomplete decomposition. To obtain a proper water depth gradient and sample as wide a range in water depths as possible, it was necessary to run a single 800-m transect from open water to dry upland, which was defined as the point at which vegetation cover changed from hydrophytic dominance to meso- / xerophytic dominance (Cowardin et al., 1979). The transect was located on the west side of Cell 3, where upland transitioned to wetland and eventually open water. It could be accessed by foot from the upland or by boat via an open channel (Figure 13). The channel was approximately 50 m wide with well-defined borders of dense *Typha x glauca* stands. It was 75 cm deep only 5 m from the shoreline, and over 1.5 m at its center. While the channel contained submerged macrophytes, it was completely devoid of emergent macrophytes, despite the ability of *T. x glauca* to thrive in water as deep as 1 m (Squires & van der Valk, 1992; Waters & Shay, 1992).

Sample sites were established every 10 m and marked with flagging tape, beginning at the edge of the open channel (sample site 0) and continuing directly west for a total of 81 sites. The precise geographic location of each site was determined using a GPS (Garmin

GPSmap 60CSx) receiver, and any observations regarding general site condition, such as evidence of muskrat activity, were recorded (Table 1 and Table 2).

Sample site water depth was measured to the nearest centimeter using a wooden meter stick pushed gently through detritus to the base of emergent macrophyte shoots. An initial water depth was measured one meter away from the transect path during its establishment. Two to four additional depths were recorded at the time of sampling from locations evenly distributed within the sampling quadrat. Where wetland plant growth was very dense, only two or three depths were measured. Several upland sites had no standing water because the water table was below ground; survey equipment was used at these sites to determine elevation relative to the water table level. Quadrat water depth measurements were recorded before any samples were collected, as removal of samples from the site often disturbed the sediment surface. An average of all measurements recorded for each site was used for analyses. The water table level was designated as 0 cm, standing water depths were recorded as negative values, while sites where the water table was below ground were given positive water depth values.

All aboveground emergent macrophyte tissue was harvested from a 0.25 m² quadrat placed approximately one meter off the transect path. The quadrat consisted of four wood slats that interlocked via notches 50 cm apart (Figure 14). When vegetation was too dense to place the fourth slat, a length of flagging tape tied to the empty notch on the third slat was strung across to the empty notch on the first slat, delineating the fourth side. Care was taken to ensure the flagging tape did not include shoots from outside the quadrat nor miss shoots originating from within it. When sample sites were located inside a sparsely vegetated muskrat clearing, the middle slat of the quadrat was tossed backward over the

shoulder and the quadrat set up where it landed, provided the location included vegetation.

Shoots were harvested from within the quadrat by cutting each shoot at its base with small pruning shears. Aboveground vegetation was separated into the following seven sample categories: *Typha* spp. (*T. x glauca* and *T. latifolia*) (1) live vegetative shoots, (2) live flowering shoots, and (3) standing dead; *Phragmites australis* (4) live shoots and (5) standing dead; *Schoenoplectus* spp. (*Schoenoplectus acutus* syn. *Scirpus acutus*, and *Schoenoplectus. tabernaemontani* syn. *Scirpus validus*) (6) live shoots and (7) standing dead. No other emergent macrophyte genera were encountered. Standing dead, sometimes referred to as aerial litter, was defined as any dead shoot angled greater than approximately 45° from the ground. Dead shoots angled less than 45° were considered litter and not sampled. Submerged detritus was also not sampled though it was necessary to remove it from many sites in order to reach shoot bases as it was often 10 to 20 cm deep.

The number and approximate mean height of shoots in each live category present were recorded. Height was measured by aligning all shoot bases from a sample and assigning a specific 25 cm height class based on the length of the majority of shoots in the sample. Height classes were defined in 25-cm increments from 1 (1.00-1.25m) to 8 (2.75-3.00m). After shoot height and number were recorded, samples were cleaned of foreign organic matter and placed in woven plastic bags for transport in the field. Samples were transferred to paper bags on the same day of sampling to allow air drying and prevent decay of samples during storage.

Flagging tape was used to mark at least three corners of the quadrat after aboveground tissue collection was complete, in order to return to the quadrat for belowground tissue sampling (Figure 15). MERP used a serrated root corer to collect belowground tissue samples; several attempts were made using the same corer at OHM but the length of transect and presence of a clay substrate made it very difficult. Instead, a 20 cm wide square-edged spade was used to create a 0.04 m² quadrat within the center of the larger previously sampled quadrat (Figure 15). Four perpendicular cuts into the sediment created the quadrat; the block of sediment and belowground tissue was removed and placed in a porous plastic bag. Roots and rhizomes were not separated. Blocks were stored at 4°C until they could be washed and dried.

The MERP root washer (Figure 16) was used to remove sediment from OHM belowground blocks. It consists of a cylindrical rotating drum set partially in a basin of water. The drum is divided into five compartments, and could therefore accommodate up to five samples. Each compartment had a lockable wire mesh opening which allowed removal of sediment without loss of root or rhizome tissue, or contamination between samples. The basin had an inlet at one end set close to the top edge and an outlet at the opposite end near the bottom of the basin. Water depth and flow rate could be controlled by increasing / decreasing the inflow and outflow accordingly. Samples were washed with tap water for ten minutes; samples from sites 30, 48, 64, and 77 required additional manual washing to remove large clumps of sediment that remained after the standard time in the root washer. Dead tissue was discarded and the clean belowground live tissue samples were returned to 4°C storage until they could be dried.

All aboveground and belowground samples were oven dried at 80°C to constant weight, usually in 48 hours for fresh samples or 24 hours for air-dried samples. Once dried, the biomass of each sample was recorded to the nearest tenth gram. Many aboveground samples were too large to dry entirely in the oven. For these, total wet weight biomass was recorded and a subsample consisting of two shoots was weighed before and after oven drying. Percent water content of the subsample was calculated and applied to the total wet weight biomass to determine the total dry weight biomass of the sample. Based on quadrat size, aboveground biomass was multiplied by four and belowground by 25 to determine biomass per m².

Two shoots from each live sample and two equivalent amounts of tissue from each dead sample were removed randomly. One subsample was retained for nutrient analysis and the other was stored as a backup. Along the entire 800 m transect, only five live and four dead *Schoenoplectus* spp. samples and three live and two dead *Phragmites* spp. samples were collected. Because of the small sample size, these data and samples were excluded from further processing and analyses. Dried *Typha* spp. subsamples were ground using a Wiley mill with a 2 mm sieve (i.e. No. 10 mesh) and stored in re-sealable plastic bags.

Table 1. Distance from open water, observations, and dates of site marking and macrophyte aboveground (AG) and macrophyte belowground (BG) sampling of the first 40 sample sites at Oak Hammock Marsh. Observations are abbreviated as follows: ch = channel, cl = clearing, e = sample site on edge of channel / clearing - random toss of quadrat not necessary, m = muskrat den clearing, rt = sample site in unvegetated area of channel / clearing - random toss of quadrat necessary, tv = terrestrial vegetation present).

Distance from Open Water (m)	Geographic Location	Site Observations	Date Site Marked	AG Sample Date	BG Sample Date
0	50°11.724N, 97°07.914W	shoreline	29/07/2013	09/08/2013	06/09/2013
10	50°11.720N, 97°07.929W		29/07/2013	09/08/2013	--
20	50°11.720N, 97°07.936W		29/07/2013	09/08/2013	--
30	50°11.716N, 97°07.945W		29/07/2013	09/08/2013	06/09/2013
40	50°11.719N, 97°07.954W		29/07/2013	09/08/2013	--
50	50°11.718N, 97°07.959W		29/07/2013	09/08/2013	--
60	50°11.714N, 97°07.966W		29/07/2013	09/08/2013	06/09/2013
70	50°11.712N, 97°07.973W	m, e	29/07/2013	09/08/2013	--
80	50°11.712N, 97°07.981W		29/07/2013	12/08/2013	--
90	50°11.718N, 97°07.989W		29/07/2013	12/08/2013	06/09/2013
100	50°11.719N, 97°07.996W		29/07/2013	12/08/2013	--
110	50°11.725N, 97°08.004W		29/07/2013	12/08/2013	--
120	50°11.726N, 97°08.011W		29/07/2013	12/08/2013	06/09/2013
130	50°11.722N, 97°08.020W		29/07/2013	12/08/2013	--
140	50°11.723N, 97°08.027W		29/07/2013	12/08/2013	--
150	50°11.724N, 97°08.036W	cl, e	29/07/2013	12/08/2013	06/09/2013
160	50°11.723N, 97°08.045W	cl, rt	29/07/2013	12/08/2013	--
170	50°11.722N, 97°08.054W		29/07/2013	12/08/2013	--
180	50°11.724N, 97°08.062W	m, e	29/07/2013	12/08/2013	06/09/2013
190	50°11.724N, 97°08.073W		29/07/2013	12/08/2013	--
200	50°11.723N, 97°08.080W	m, e	29/07/2013	12/08/2013	--
210	50°11.721N, 97°08.089W		29/07/2013	13/08/2013	06/09/2013
220	50°11.722N, 97°08.096W		29/07/2013	13/08/2013	--
230	50°11.721N, 97°08.104W		29/07/2013	13/08/2013	--
240	50°11.722N, 97°08.113W		29/07/2013	13/08/2013	05/09/2013
250	50°11.722N, 97°08.121W		29/07/2013	13/08/2013	--
260	50°11.722N, 97°08.129W		29/07/2013	13/08/2013	--
270	50°11.720N, 97°08.137W		29/07/2013	13/08/2013	05/09/2013
280	50°11.721N, 97°08.145W		29/07/2013	13/08/2013	--
290	50°11.722N, 97°08.154W		29/07/2013	13/08/2013	--
300	50°11.722N, 97°08.162W	m, e	29/07/2013	13/08/2013	05/09/2013
310	50°11.721N, 97°08.171W	cl, e	29/07/2013	15/08/2013	--
320	50°11.720N, 97°08.179W		29/07/2013	15/08/2013	--
330	50°11.721N, 97°08.187W		29/07/2013	15/08/2013	05/09/2013
340	50°11.721N, 97°08.195W		29/07/2013	15/08/2013	--
350	50°11.721N, 97°08.204W		29/07/2013	15/08/2013	--
360	50°11.721N, 97°08.211W		29/07/2013	15/08/2013	05/09/2013
370	50°11.722N, 97°08.220W		29/07/2013	15/08/2013	--
380	50°11.723N, 97°08.227W		29/07/2013	15/08/2013	--
390	50°11.721N, 97°08.236W		29/07/2013	15/08/2013	05/09/2013
400	50°11.720N, 97°08.244W		29/07/2013	15/08/2013	--

Table 2. Distance from open water, observations, and dates of site marking and macrophyte aboveground (AG) and macrophyte belowground (BG) sampling of the last 40 sample sites at Oak Hammock Marsh. Observations are abbreviated as follows: ch = channel, cl = clearing, e = sample site on edge of channel / clearing - random toss of quadrat not necessary, m = muskrat den clearing, rt = sample site in unvegetated area of channel / clearing - random toss of quadrat necessary, tv = terrestrial vegetation present).

Distance from Open Water (m)	Geographic Location	Site Observations	Date Site Marked	AG Sample Date	BG Sample Date
410	50°11.722N, 97°08.251W		29/07/2013	15/08/2013	--
420	50°11.724N, 97°08.259W	ch, e	29/07/2013	15/08/2013	05/09/2013
430	50°11.722N, 97°08.268W	ch, e	29/07/2013	15/08/2013	--
440	50°11.720N, 97°08.277W		29/07/2013	15/08/2013	--
450	50°11.721N, 97°08.285W		29/07/2013	15/08/2013	05/09/2013
460	50°11.723N, 97°08.292W		31/07/2013	19/08/2013	--
470	50°11.722N, 97°08.300W		31/07/2013	19/08/2013	--
480	50°11.721N, 97°08.308W		31/07/2013	19/08/2013	05/09/2013
490	50°11.722N, 97°08.316W		31/07/2013	19/08/2013	--
500	50°11.721N, 97°08.325W		31/07/2013	19/08/2013	--
510	50°11.721N, 97°08.332W		31/07/2013	19/08/2013	05/09/2013
520	50°11.721N, 97°08.341W	cl, e	31/07/2013	19/08/2013	--
530	50°11.725N, 97°08.347W		31/07/2013	19/08/2013	--
540	50°11.724N, 97°08.354W		31/07/2013	19/08/2013	28/08/2013
550	50°11.725N, 97°08.362W		31/07/2013	19/08/2013	--
560	50°11.724N, 97°08.371W		31/07/2013	19/08/2013	28/08/2013
570	50°11.725N, 97°08.378W		31/07/2013	19/08/2013	--
580	50°11.725N, 97°08.385W		31/07/2013	19/08/2013	28/08/2013
590	50°11.725N, 97°08.394W		31/07/2013	19/08/2013	--
600	50°11.724N, 97°08.404W		31/07/2013	14/08/2013	28/08/2013
610	50°11.725N, 97°08.411W	cl, e	31/07/2013	14/08/2013	--
620	50°11.724N, 97°08.419W	cl, rt	31/07/2013	14/08/2013	28/08/2013
630	50°11.724N, 97°08.427W		31/07/2013	14/08/2013	--
640	50°11.724N, 97°08.435W		31/07/2013	14/08/2013	28/08/2013
650	50°11.724N, 97°08.444W		31/07/2013	14/08/2013	--
660	50°11.722N, 97°08.452W		31/07/2013	14/08/2013	28/08/2013
670	50°11.723N, 97°08.460W		31/07/2013	14/08/2013	--
680	50°11.724N, 97°08.469W		31/07/2013	14/08/2013	28/08/2013
690	50°11.723N, 97°08.477W	cl, e	31/07/2013	14/08/2013	--
700	50°11.723N, 97°08.486W	cl, e	31/07/2013	14/08/2013	--
710	50°11.724N, 97°08.494W		31/07/2013	21/08/2013	07/09/2013
720	50°11.724N, 97°08.502W		31/07/2013	21/08/2013	--
730	50°11.724N, 97°08.513W		31/07/2013	21/08/2013	--
740	50°11.723N, 97°08.522W		31/07/2013	21/08/2013	07/09/2013
750	50°11.724N, 97°08.529W		31/07/2013	21/08/2013	--
760	50°11.722N, 97°08.537W		31/07/2013	21/08/2013	--
770	50°11.724N, 97°08.546W		31/07/2013	21/08/2013	07/09/2013
780	50°11.724N, 97°08.554W	tv	31/07/2013	21/08/2013	--
790	50°11.722N, 97°08.562W	tv	31/07/2013	21/08/2013	--
800	50°11.723N, 97°08.570W	tv	31/07/2013	21/08/2013	07/09/2013
810	--	upland	--	--	--

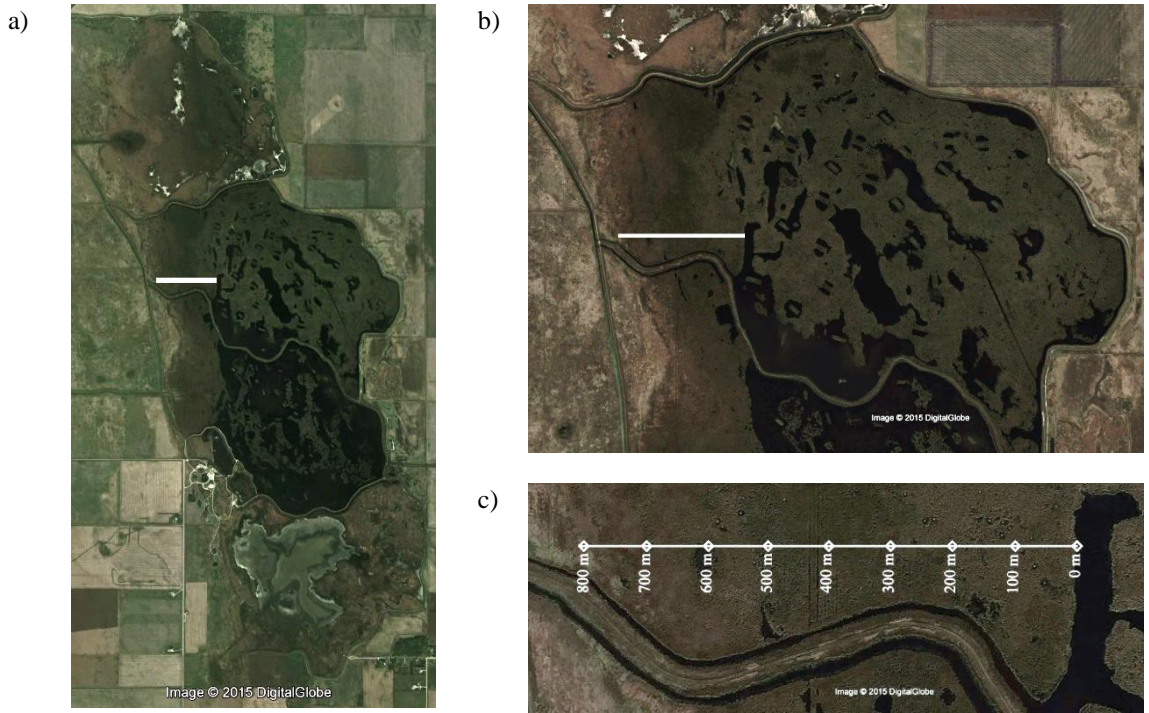


Figure 13. Oak Hammock Marsh (a) wetland complexes, (b) Cell 3, and (c) sampling transect (Source: Google™ Earth, ©DigitalGlobe, 2015, Image Date 25/9/2015).

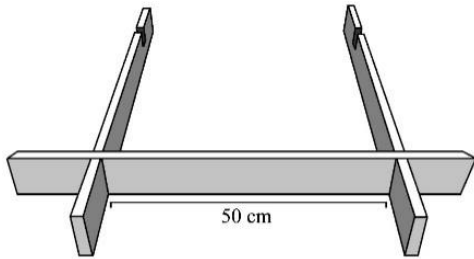


Figure 14. Wooden quadrat (50 cm x 50 cm) for emergent macrophyte sampling.

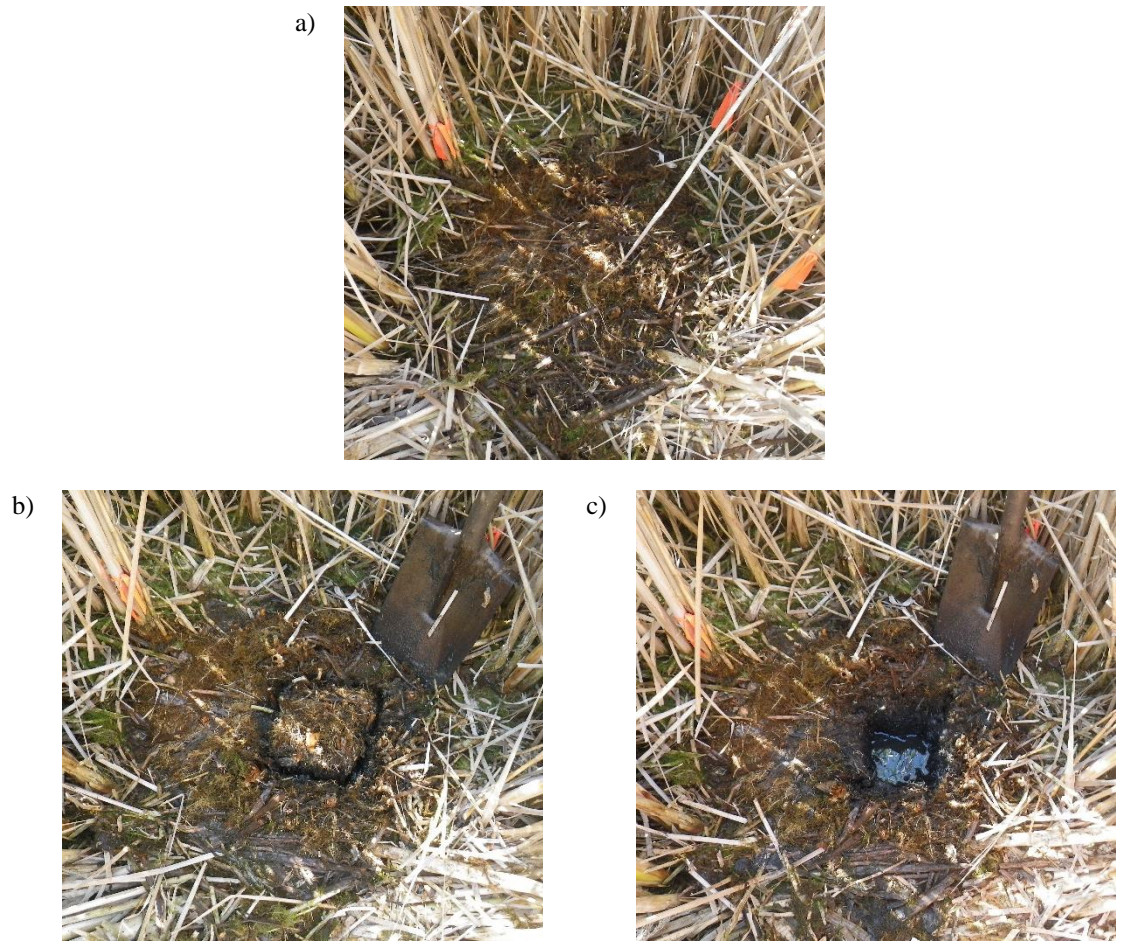


Figure 15. Emergent macrophyte (a) quadrat cleared of aboveground live and dead tissue, and belowground tissue sample block (b) marked out, and (c) removed at Cell 3, Oak Hammock Marsh, Canada, 2013.



Figure 16. Marsh Ecology Research Program (a) root washer, (b) sample compartment, and (c) rotating compartment drum.

3.2.3. Laboratory Analysis

Kjeldahl Digestion

Ground plant tissue samples were digested using a modified Kjeldahl wet oxidation method (Parkinson & Allen, [1975](#)) following the standard operating procedures of the Flaten laboratory in Department of Soil Sciences, University of Manitoba.

A 0.4 g portion of ground sample or reference material was transferred to a dry 100 mL Kjeldahl tube for digestion. One digest run included up to 37 ground samples and the following three quality control measures: a replicate of the last ground sample, a blank to contain digest solution only, and a certified reference material of citrus leaves (NIST, [1982](#)). Immediately before digestion, 4.4 mL of digest solution was added to each Kjeldahl tube. The digest solution used was that described by Parkinson & Allen ([1975](#)) who concluded their recommended procedure fully breaks down plant tissue bringing P, organic N, and ammoniacal-N completely into solution and is therefore suitable for both N and total P analysis. It should be noted that sulfuric acid and hydrogen peroxide concentrations used in the digest solution were 99.99% and 30% respectively, and the digest solution was prepared in an ice bath using P-free chemicals and stored at 2°C (Akinremi et al., [2003](#)).

After addition of the digest solution, Kjeldahl tubes were heated according to a temperature schedule outlined by Akinremi et al. ([2003](#)). Seven digests were run using two batches of digest solution. All equipment and glassware was cleaned using distilled deionized water between digests.

Kjeldahl tubes were removed from the digest block after the prescribed period of time and cooled to room temperature. Sample digests were then transferred to 50 mL volumetric flasks by thoroughly and repeatedly washing each tube with distilled deionized water. Flasks were made to volume and the digests transferred to plastic vials and stored at 4°C prior to quantitation.

Phosphorus

Total reactive phosphorus (i.e. orthophosphate ($\text{PO}_4\text{-P}$); hereafter TP) was determined via colorimetric analysis of the Kjeldahl sample digests using standard ascorbic acid methods (APHA, [1992a](#)). For each sample, including all quality controls, a 0.5 mL aliquot of digest was transferred to a 25 mL volumetric flask, to which 4 mL of fresh ascorbic acid reagent was added, made to volume with distilled deionized water, and mixed by inverting. Samples with insufficiently low TP concentrations were identified as those with little to no blue colour development within 15 minutes of mixing the flask. In these cases, a 5 mL aliquot of the sample digest was transferred to a new volumetric flask and neutralized with 1 mL of 10 molar sodium hydroxide (NaOH) before adding the reagent. Seven P standards, ranging from 0 to 1.0 $\mu\text{g P/mL}$, were prepared fresh daily and used to create calibration curves. Colour was allowed to develop for at least 15 minutes at which point each sample was transferred to a 1 cm cuvette and its absorbance read at 882 nm using a Biochrom™ Ultrospec 2100 Pro UV/Visible Spectrophotometer. According to standard methods, the minimum detectable concentration was approximately 0.15 $\mu\text{g P/mL}$ using a 1 cm light path.

Total Kjeldahl Nitrogen

Total Kjeldahl nitrogen (i.e. organic and ammoniacal-nitrogen; hereafter TKN) was determined via colorimetric analysis of the Kjeldahl sample digests using standard automated phenate methods (APHA, [1992b](#)). An aliquot of each sample and quality control digest was diluted 100-fold using a Hamilton MicroLab® Controller prior to analysis. A Technicon® AutoAnalyzer II continuous flow autoanalyzer was used to measure diluted sample absorbance at 630 nm. Each analysis began with a combination of washes using reverse osmosis water, 7 calibrants ranging from 0 to 3.6 µg N/mL, rinses with distilled deionized water, and a low and high quality control. To maintain instrument accuracy, a rinse with distilled deionized water, a gain using 1 µg N/mL to correct any drift, and a second rinse followed every 20 samples. Peak analysis was conducted using Labtronics Inc. New Analyzer Program (v 4.4) software. According to standard methods, the minimum detectable concentration was approximately 0.005 µg N/mL.

Total Nitrogen

Total nitrogen (i.e. organic N, ammoniacal N, nitrite, and nitrate, hereafter TN) was determined via combustion using the standard operating procedures of the Stainton laboratory in Department of Fisheries and Oceans, Winnipeg, Canada.

Small amounts of each sample were weighed into 6 x 4 mm tin capsules using a Perkin-Elmer Ad-6 Autobalance, accurate to 0.001 mg. An Exeter Analytical Inc. CE-440 elemental analyzer and its associated software, Linear Regression Plus, were used to determine TN of each sample. The analyzer was unable to determine TN for samples with large amounts of carbon, usually a result of too much sample in the tin capsule, but

too small a sample yielded erroneous results. To determine optimal mass, a trial run was conducted in which each sample type was analyzed five times using masses ranging from 2.000 mg to 7.000 mg. The following are the target masses determined from the trial: approximately 3.500 to 4.500 mg of vegetative, 5.500 to 6.500 mg of flowering, 3.000 to 4.000 mg of belowground, and 4.000 to 5.000 mg of dead tissue. According to standard methods, the minimum detectable concentration was approximately 0.001 mg N per sample analysis.

Every tenth sample was analyzed in triplicate to confirm continued precision of the analyzer and if samples were ground finely enough to be considered homogenous. All replicates were within two standard deviations and fell within a 95% confidence interval of their respective mean so it was concluded that samples were sufficiently homogenous and did not need additional grinding. This confirmation was essential as OHM samples were ground to pass through a 2 mm sieve (i.e. No. 10 mesh) whereas MERP samples were passed through a 0.149 mm sieve (i.e. No. 100 mesh) and sample homogeneity was needed to insure comparable results. Mean values were used where triplicate analysis was conducted. Dead tissue TN analysis was conducted for every other sample site.

MERP did not conduct TKN analyses of plant samples; they conducted analyses for TN only. The two should not be confused, though they are often used interchangeably. TKN analyzes samples for organic and ammoniacal-N, whereas TN analysis includes nitrate and nitrite in its analysis. This study conducted analyses of both TKN and TN to provide an opportunity to assess how similar TKN and TN content is in emergent macrophytes.

3.2.4. Data Analysis

Vegetative and flowering shoots were not separated during MERP sampling; therefore, an additional *Typha* spp. category comprised of all aboveground live growth was created by combining the results from laboratory analyses for vegetative and flowering *Typha* spp. For all sample types, biomass and nutrient concentration were used to determine the mass of N and P per m² to investigate the nutrient sequestration potential of *Typha* stands at OHM. These values, as well as aboveground to belowground biomass allocation, were compared to water depth to investigate what, if any, relationships existed. TN to TP ratios were calculated to investigate nutrient limitation as per Koerselman & Meuleman (1996). TN to TKN ratios were calculated to explore their relationship. A value close or equal to one indicates that all N in the tissue is organic, whereas values less than one indicate that some N is stored as nitrate or nitrite in the plant tissue.

Linear regression analyses were conducted to investigate potential relationships between measured variables as well as between each variable and both water depth and sample site location. Tukey-Kramer analyses were used to determine if mean values of tissue types for a given parameter were significantly different. Measure of variability around mean values was estimated using standard deviation. All statistical analyses were conducted using an alpha value of 0.1. Statistical analyses were conducted using Microsoft® Excel 2013 and JMP® 10.

3.3. Results

Water Depth Profile

Standing water reached a maximum depth of 55 cm, while the water level was as much as 6 cm belowground in the upland; the transect therefore covered a 61 cm range in water depth. The emergent macrophyte stand had a depth of 20 cm at open water (i.e. site 0 m), where its dense vegetation ended abruptly, with no transitional zone between it and the adjacent open channel. The channel was approximately 50 m wide, 75 cm deep only 5 m from the emergent macrophyte stand, and well over 1 m deep at the center.

A water-depth profile of the transect (Figure 17) showed that depth decreased for the first 400 m, followed by a marked increase until approximately 620 m from open water, after which it decreased again until the water surface was below ground in the upland. The profile also showed numerous abrupt changes in water depth (e.g. 350 m and 420 m) and that these micro-fluctuations in bathymetry / topography were found along the entire transect, resulting in a very complex water-depth gradient. However, linear regression analysis of the relationship between water depth and distance from open water revealed that it was statistically significant ($p < 0.0001$, $R^2 = 0.372$) with a positive slope, and that the transect had a 0.04% gain in elevation moving towards the upland. Because the relationship was significant, distance from open water is used in the following results and discussion as a proxy for water depth along a water depth gradient, with increasing distance from open water corresponding to decreasing water depth.

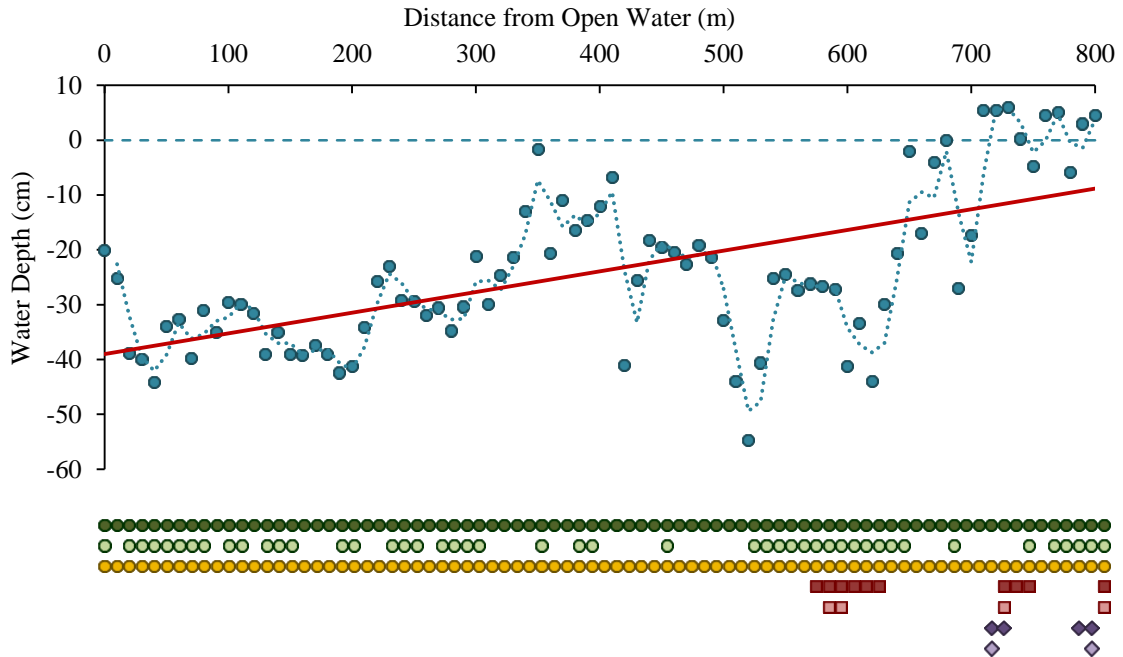


Figure 17. Sample site water depth (●) (wetland water surface = 0 cm (---)) from dry upland (800 m from open water) to deep water (0 m from open water) and the general water depth gradient (— $p < 0.0001$, $R^2 = 0.372$, $n = 81$), including presence of *Typha* spp. live vegetative (●), live flowering (○), and standing dead (●) shoots, *Schoenoplectus* spp. live shoots (■) and standing dead (□), and *Phragmites australis* live shoots (◆) and standing dead (◆) in Cell 3 of Oak Hammock Marsh, Manitoba, 2013.

Emergent Macrophyte Species Distribution

Only three emergent macrophyte taxa were encountered along the transect. *Typha* spp. was the most frequent; vegetative shoots and standing dead were found at all 81 sites while flowering shoots were found at 46 sites along the length of the entire transect (Figure 17). *Typha* was therefore found at depths ranging from 55 cm to 6 cm above the water table level (Table 3). Live *Schoenoplectus* spp. shoots were found at four sites in the upland and six sites in deeper water approximately 200 m further in to the wetland, though not at similar depths elsewhere on the transect. Four of the ten sites also contained dead *Schoenoplectus* shoots (Figure 17). The water depth of *Schoenoplectus* ranged from 44 cm to 6 cm above the water table level. *Phragmites australis* was encountered least often, with only four and two upland sites containing live and dead shoots, respectively.

Its water depth ranged from 6 cm to 6 cm above the water table level (Table 3). As *Typha* was the only taxon present at a sufficient number of sample sites to allow for statistical analysis, its samples were the only ones analyzed for biomass and nutrient content.

Table 3. Sample site and water depth range of emergent macrophyte species in Cell 3 of Oak Hammock Marsh, Canada, 2013, where sample site 0 is at the edge of open water and 800 is in dry upland, and positive water depth values indicate a belowground water table level.

Emergent Macrophyte Species	Sample Site	Water Depth (cm)
<i>Typha x glauca</i>	0 to 800	-55 to 6
<i>Schoenoplectus</i> spp.	570 to 800	-44 to 6
<i>Phragmites australis</i>	710 to 790	-6 to 6

Growth Performance

Mean dry weight biomass per square meter of aboveground live, aboveground dead, and belowground *Typha x glauca* tissues were all significantly different ($p < 0.0001$). On average, belowground biomass was the highest, while aboveground live biomass was the least (Table 4). Minimum and maximum aboveground live biomasses were 127.6 and 1865.3 g/m², respectively, while the average was 821 ± 393 g/m².

Aboveground live and dead biomass increased significantly as water depth increased ($p = 0.06$ and $p < 0.0001$, respectively), while belowground biomass decreased significantly ($p = 0.05$) (Table 4, Figure 18). Total live biomass (i.e. aboveground and belowground combined) was not significantly related to water depth ($p = 0.11$) (Table 4). Biomass of all three tissue types showed a higher degree of variation in deeper water than shallow (Figure 18).

Typha had an average of 12.6 ± 5.4 live shoots per square meter. Number of shoots was not statistically related to water depth ($p = 0.21$) (Table 4). An average of $33 \pm 14\%$ of total live tissue per square meter (i.e. aboveground live and belowground tissue) was allocated

to aboveground growth; this percentage increased significantly with increasing water depth ($p=0.05$), from approximately 20% in the upland to 50% near open water (Table 4, Figure 19). Mean shoot height increased with increasing water depth ($p<0.0001$) (Table 4, Figure 20).

Table 4. Mean (standard deviation) biomass, TP, TKN, TN, TN to TKN ratio, and TN to TP ratio of *Typha x glauca* aboveground live (AGL), belowground live (BG), aboveground dead (AGD), and total live (TL) tissue in Cell 3 of Oak Hammock Marsh, Canada, 2013, and their relationship to sample site water depth and location along a water depth gradient.

Tissue Type	n	Mean (SD)	Relationship to Water Depth			Relationship to Location			
			R ²	Slope	p-value	R ²	Slope	p-value	
Biomass (g/m ²)	AGL	69	821 (393)	0.047	+	*0.0739	0.051	+	*0.0616
	BG	30	1936 (1267)	0.001		0.8973	0.127	–	*0.0530
	AGD	79	1248 (559)	0.026		0.1566	0.234	+	***<0.0001
	TL	26	2754 (1481)	0.012		0.5993	0.105		0.1068
TP (mg/g)	AGL	69	1.5 (0.3)	0.042	+	*0.0903	0.107	+	***0.0062
	BG	30	1.1 (0.4)	0.010		0.4600	0.125	+	*0.0553
	AGD	78	0.3 (0.1)	0.016		0.2751	0.045	–	*0.0608
TP (g/m ²)	AGL	69	1.2 (0.6)	0.075	+	**0.0229	0.132	+	***0.0022
	BG	30	2.0 (1.2)	0.007		0.6565	0.031		0.3512
	AGD	78	0.4 (0.3)	0.003		0.6562	0.033		0.1115
TKN (mg/g)	AGL	66	11.8 (2.3)	0.076	+	**0.0247	0.096	+	**0.0113
	BG	30	8.4 (2.5)	0.537	–	***<0.0001	0.207	–	**0.0116
	AGD	78	3.5 (0.8)	0.001		0.7621	0.013		0.3123
TKN (g/m ²)	AGL	66	9.4 (5.1)	0.088	+	**0.0158	0.133	+	***0.0026
	BG	30	16.6 (12.6)	0.100	–	*0.0883	0.240	–	***0.0060
	AGD	78	4.3 (2.3)	0.025		0.1667	0.146	+	***0.0006
TN (mg/g)	AGL	63	14.0 (2.6)	0.096	+	**0.0134	0.071	+	**0.0350
	BG	30	10.2 (2.8)	0.561	–	***<0.0001	0.248	–	***0.0051
	AGD	41	6.2 (0.9)	0.102	+	**0.0420	0.000		0.9944
TN (g/m ²)	AGL	63	11.2 (6.3)	0.081	+	**0.0235	0.115	+	***0.0065
	BG	30	20.3 (15.0)	0.085		0.1172	0.251	–	***0.0048
	AGD	41	7.7 (3.9)	0.014		0.4609	0.138	+	**0.0167
TN:TKN	AGL	63	1.2 (0.1) ^A	0.000		0.9341	0.005		0.5866
	BG	30	1.2 (0.1) ^A	0.012		0.5658	0.003		0.7601
	AGD	41	1.8 (0.2)	0.075	+	*0.0826	0.073	+	*0.0880
TN:TP	AGL	63	20.4 (2.9) ^B	0.007		0.5228	0.028		0.1938
	BG	30	22.9 (11.3) ^B	0.255	–	***0.0045	0.277	–	***0.0028
	AGD	41	50.2 (14.1)	0.261	+	***0.0006	0.158	+	***0.0099
Shoot Height (m)	80	2.00 – 2.25	0.063	+	**0.0244	0.180	+	***<0.0001	
# of Shoots / m ²	81	12.6 (5.4)	0.005		0.5108	0.020		0.2059	
AGL % of TL Biomass	26	33 (14)	0.080		0.1627	0.152	+	**0.0487	

Superscript letters indicate mean values that are not significantly different. Significant relationships between measured parameter and water depth or location are indicated by asterisks, where ***, **, and * indicate significance at α levels of 0.01, 0.05, and 0.1, respectively. When significant, + indicates a positive slope (value increases as water depth increases / move towards open water), and – indicates negative slope (values decrease as water depth increases / move towards open water).

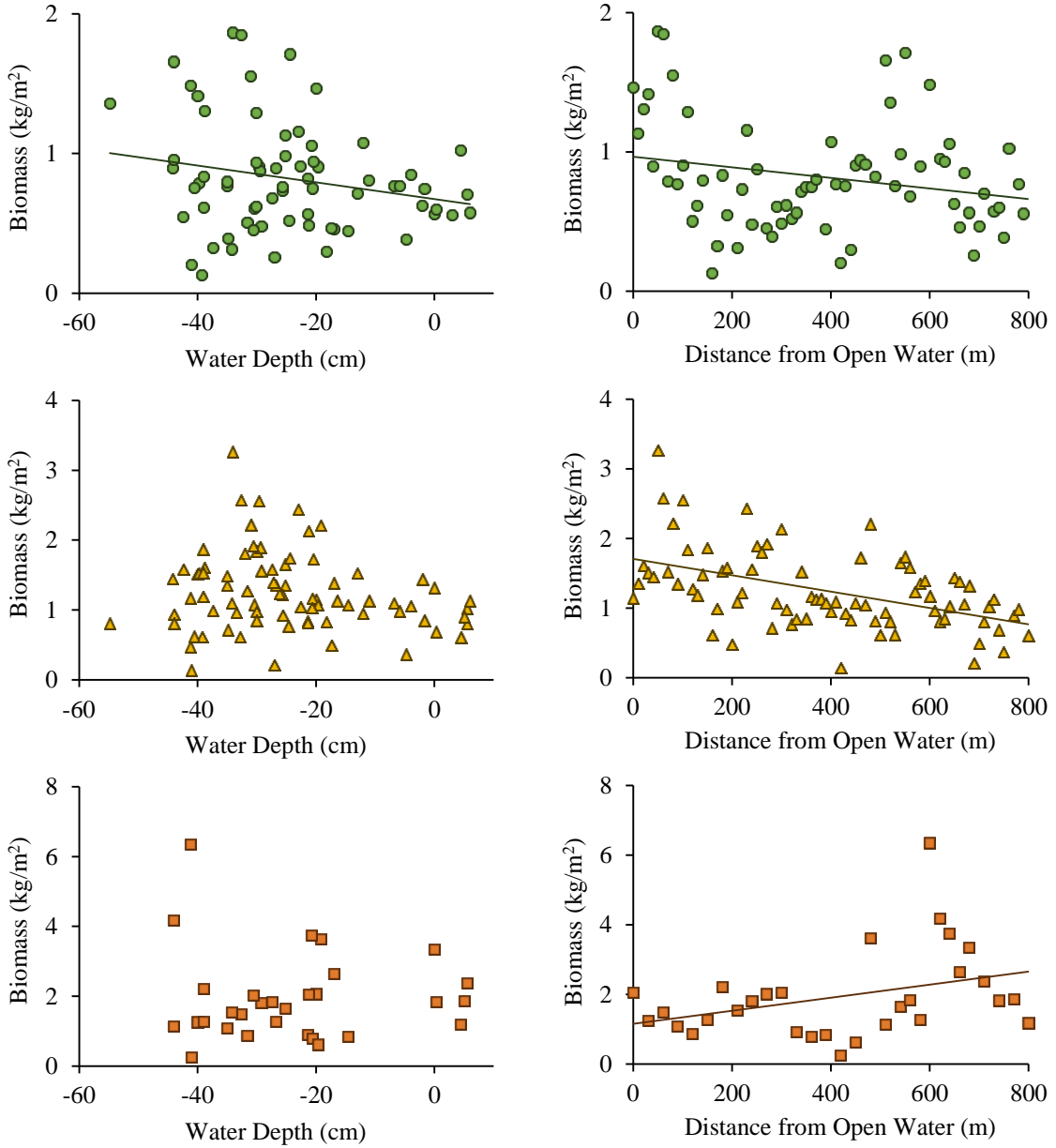


Figure 18. Aboveground live (n=69) (●), aboveground dead (n=79) (▲), and belowground (n=30) (■) *Typha x glauca* biomass (kg/m²) by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

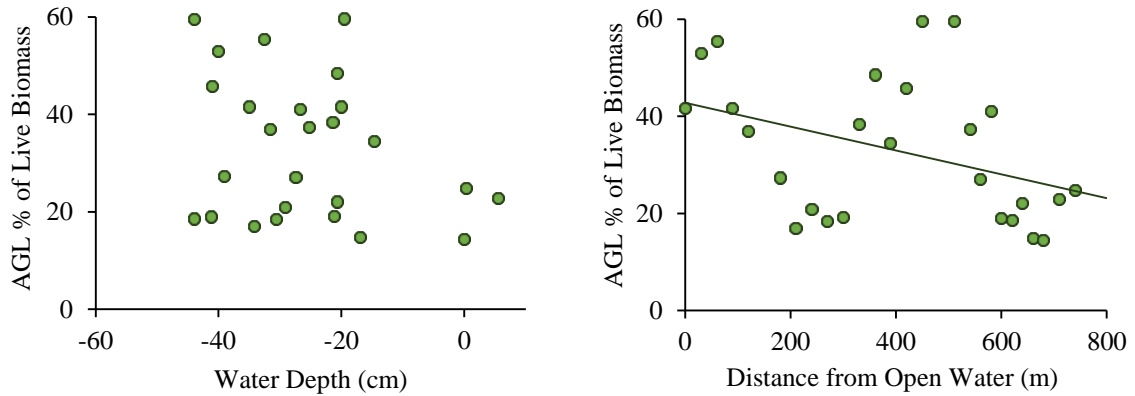


Figure 19. Percent biomass allocation to aboveground growth of *Typha x glauca* (n=26) by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

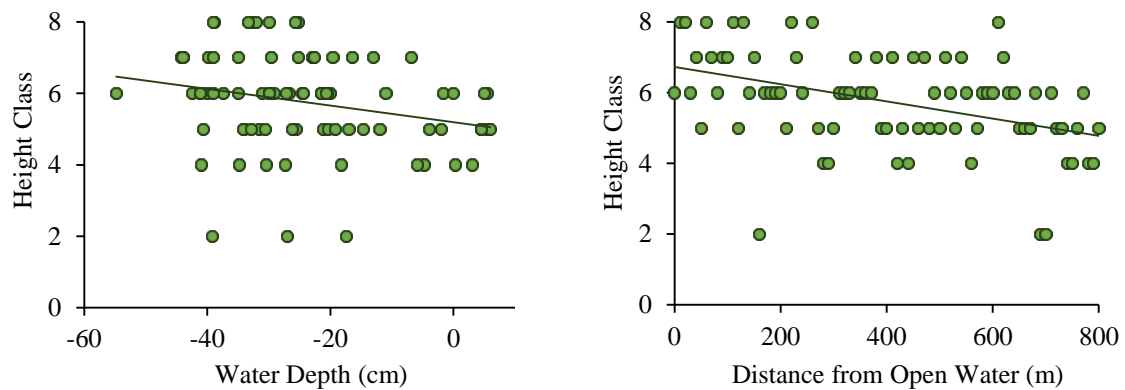


Figure 20. *Typha x glauca* shoot height (n=80) by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines; height classes were defined in 25-cm increments from 1 (1.00-1.25 m) to 8 (2.75-3.00m)).

Nutrient Content

Aboveground live, aboveground dead, and belowground *Typha x glauca* tissue contained significantly different concentrations of each nutrient ($p<0.0001$) (Table 4). Aboveground live *T. x glauca* tissue contained the highest concentrations of all nutrients (1.5 ± 0.3 mg P/g, 11.8 ± 2.3 mg TKN/g; 14.0 ± 2.6 mg TN/g), but because of differences in biomass belowground tissue accounted for the largest amount of each nutrient per square meter

(2.0 ± 1.2 g TP/m²; 16.6 ± 12.6 g TKN/m²; 20.3 ± 15.0 g TN/m²) (Table 4). Aboveground dead had the lowest concentrations and accounted for the least amounts of each nutrient (Table 4).

Aboveground live and belowground tissue TP concentrations increased significantly with increasing water depth ($p=0.006$ and $p=0.06$, respectively). In contrast, aboveground dead TP concentration decreased significantly ($p=0.06$) (Table 4, Figure 21). Amount of P per square meter increased significantly with increasing water depth for aboveground live tissue only ($p=0.002$) (Table 4, Figure 22).

Both TKN concentration and amount per square meter in aboveground live *T. glauca* tissue increased significantly with increasing water depth ($p=0.01$ and $p=0.003$, respectively), while the opposite relationship was observed in belowground tissue ($p=0.01$ and $p=0.01$, respectively). Aboveground dead TKN concentration was unrelated to water depth though amount per square meter in that tissue significantly increased ($p=0.31$ and $p=0.0006$) (Table 4, Figure 23, Figure 24).

Aboveground live tissue TN concentration and amount per square meter increased significantly with increasing water depth ($p=0.04$ and $p=0.007$, respectively) (Table 4, Figure 25, Figure 26). In contrast, belowground concentration and amount per square meter decreased significantly ($p=0.005$ and $p=0.005$, respectively) (Table 4, Figure 25, Figure 26). Aboveground dead TN concentration was unrelated water depth ($p=0.99$) but amount per square meter increased significantly with depth ($p=0.02$) (Table 4, Figure 25, Figure 26).

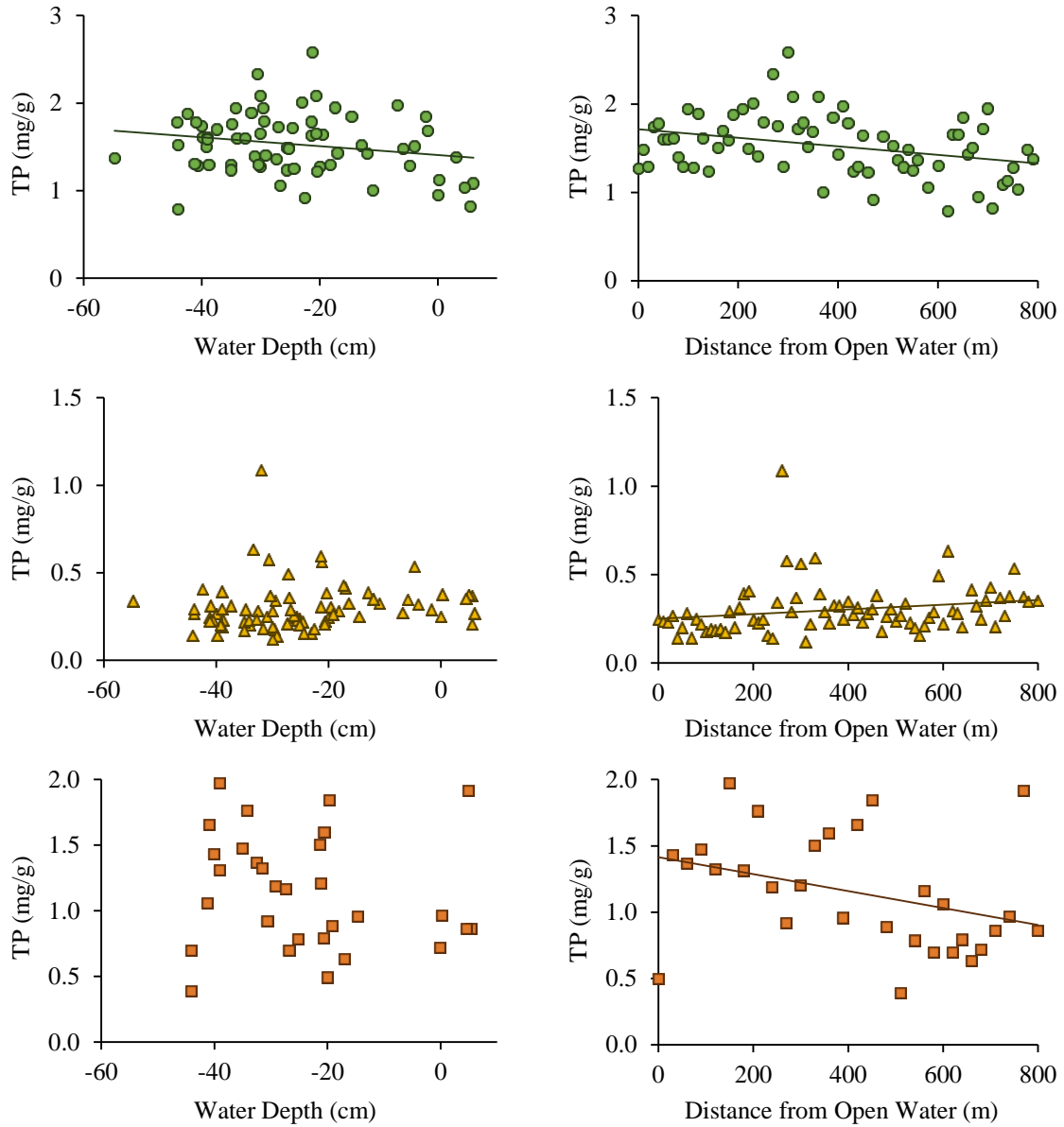


Figure 21. TP concentration (mg/g) in aboveground live (n=69) (●), aboveground dead (n=78) (▲), and belowground (n=30) (■) *Typha x glauca* tissue by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

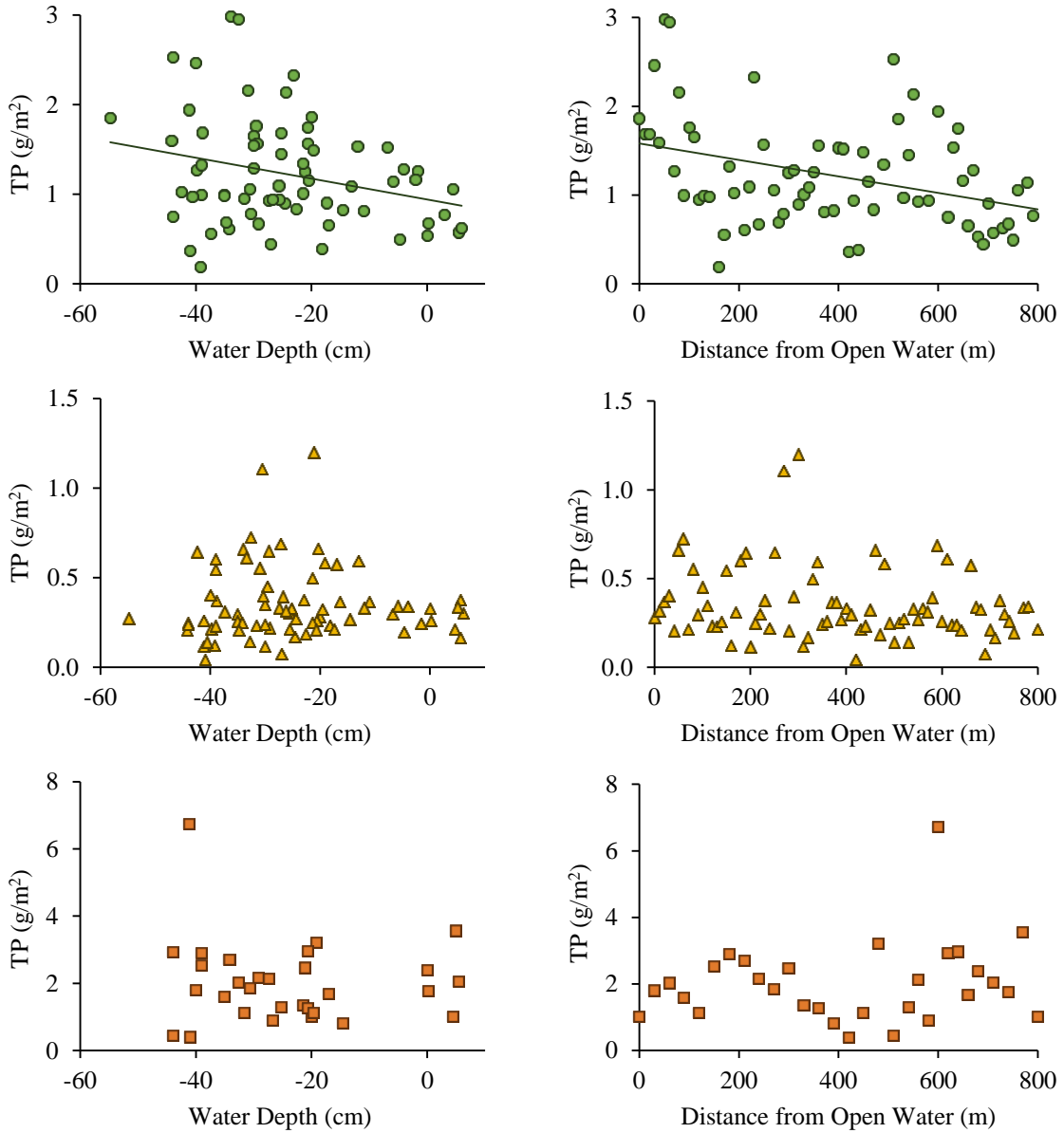


Figure 22. TP per square meter (g/m^2) in aboveground live ($n=69$) (●), aboveground dead ($n=78$) (▲), and belowground ($n=30$) (■) *Typha x glauca* tissue by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

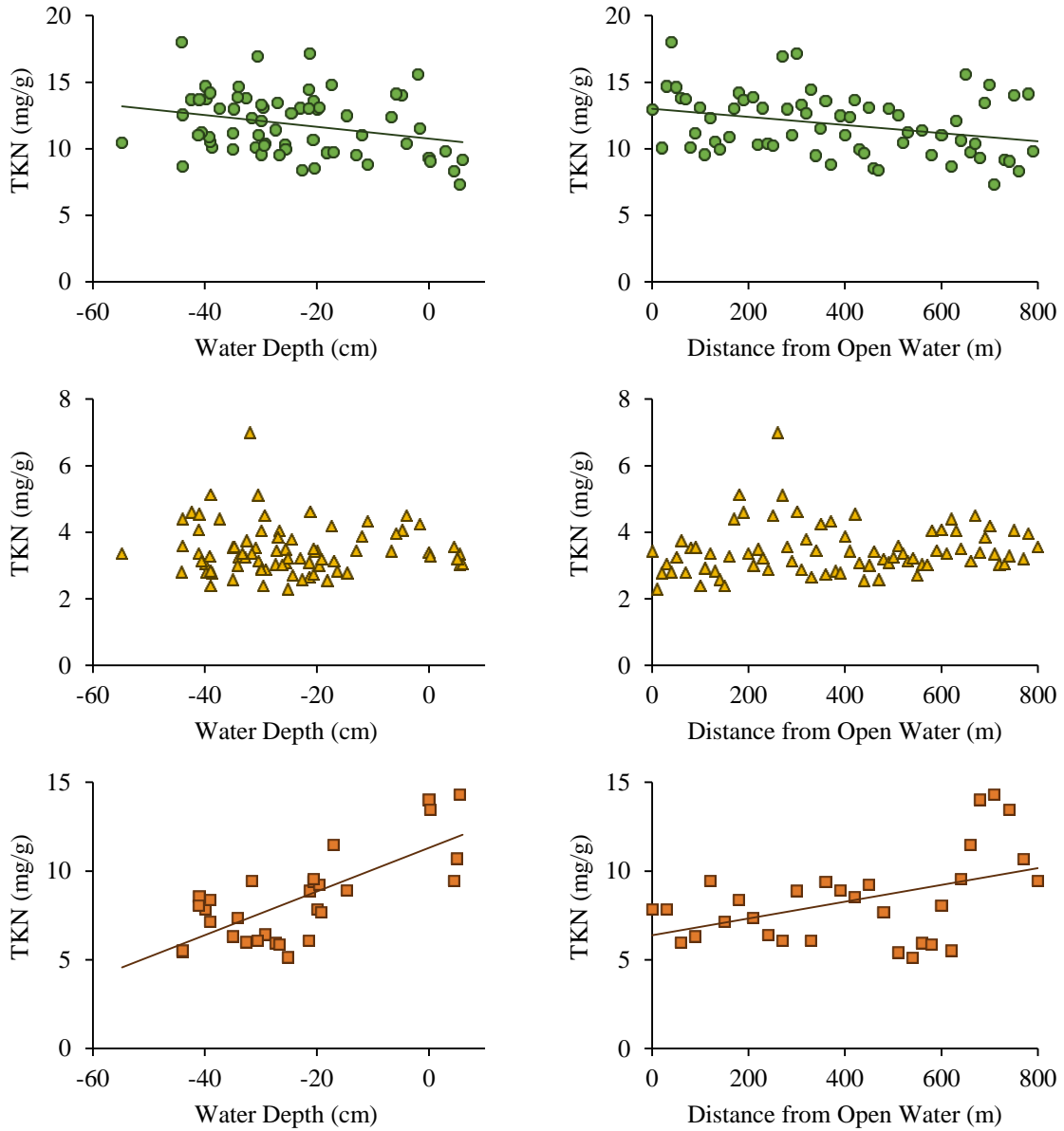


Figure 23. TKN concentration (mg/g) in aboveground live (n=66) (●), aboveground dead (n=78) (▲), and belowground (n=30) (■) *Typha x glauca* tissue by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

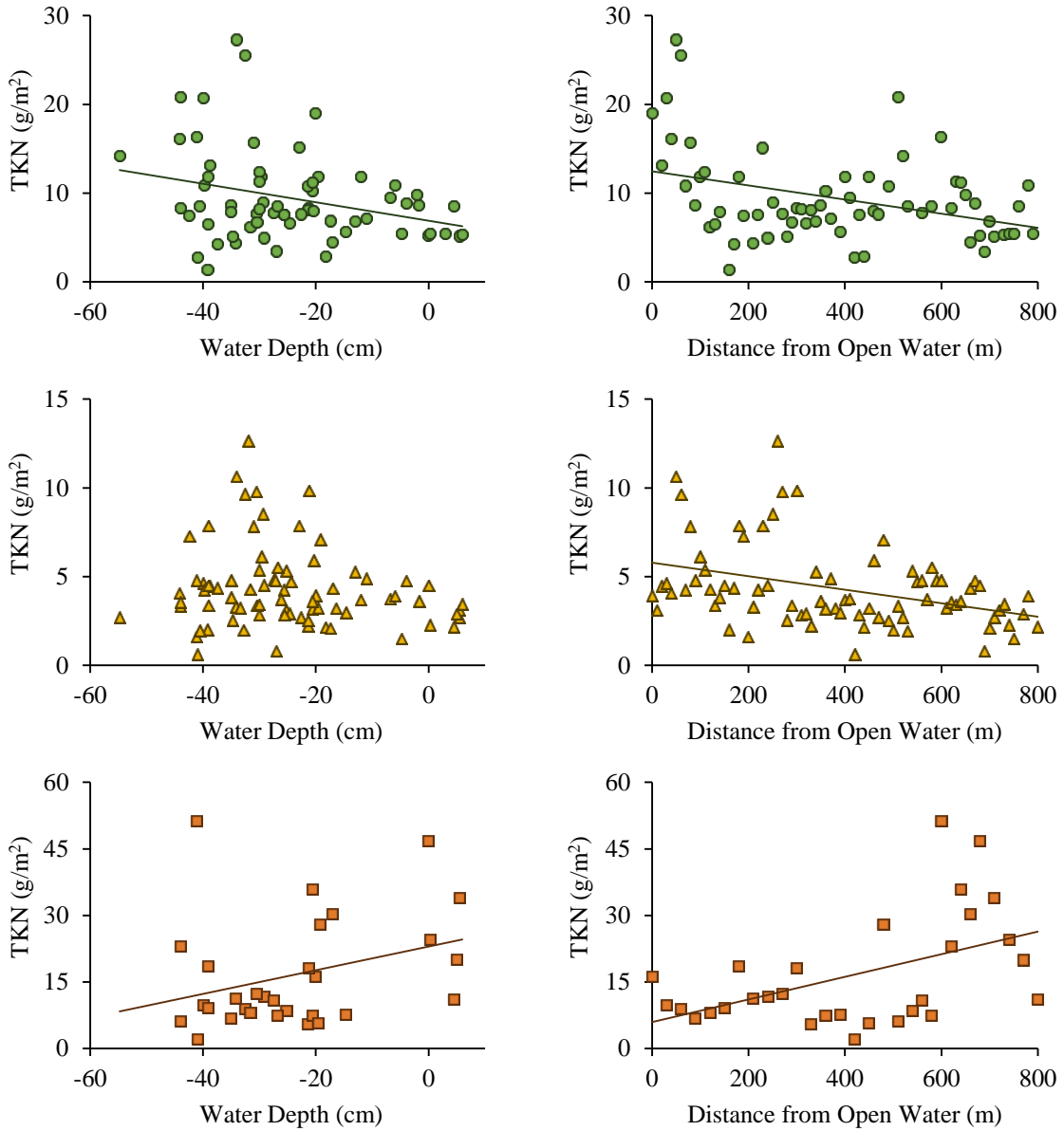


Figure 24. TKN per square meter (g/m^2) in aboveground live ($n=66$) (●), aboveground dead ($n=78$) (▲), and belowground ($n=30$) (■) *Typha x glauca* tissue by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

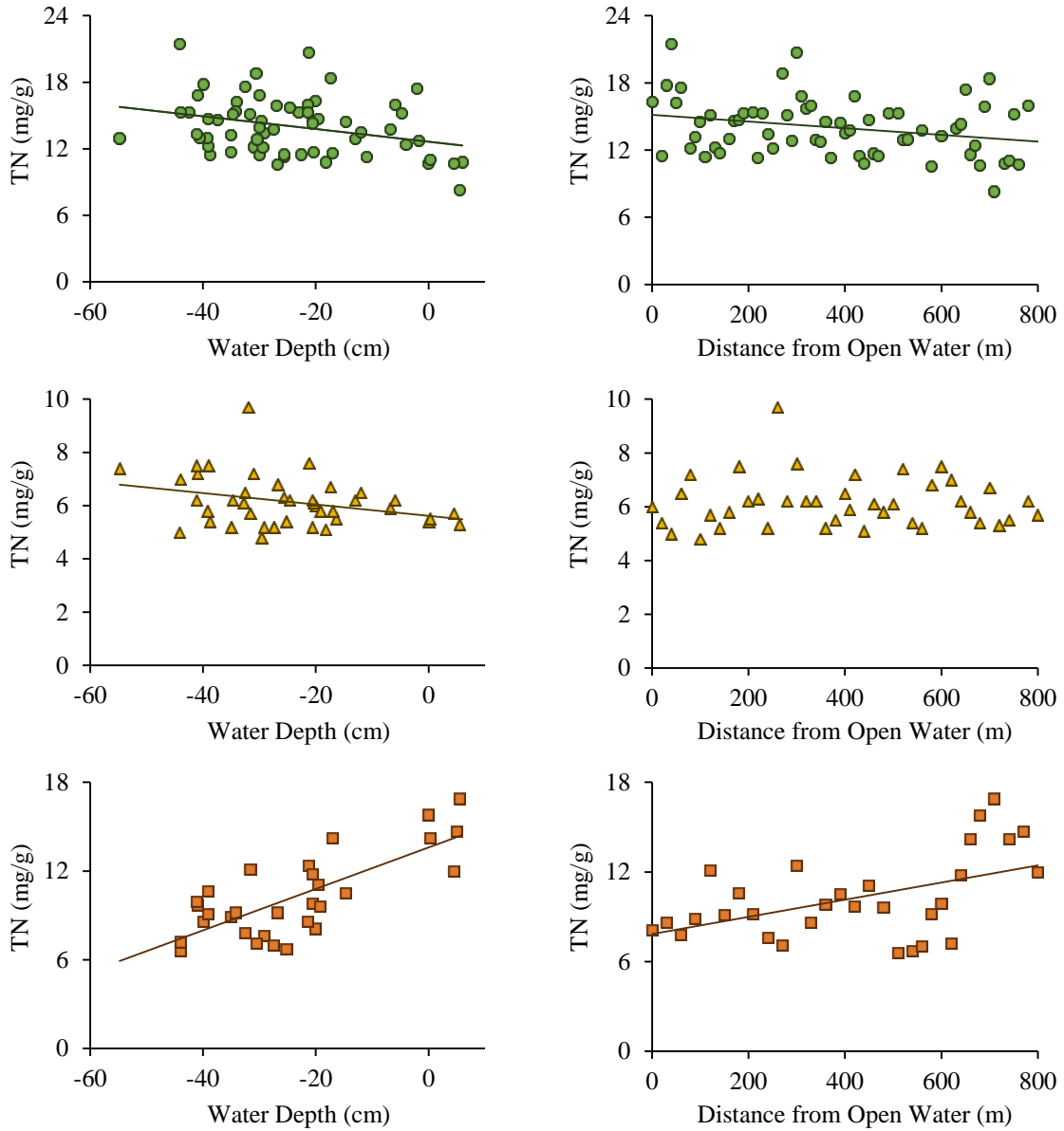


Figure 25. TN concentration (mg/g) in aboveground live (n=63) (●), aboveground dead (n=41) (▲), and belowground (n=30) (■) *Typha x glauca* tissue by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

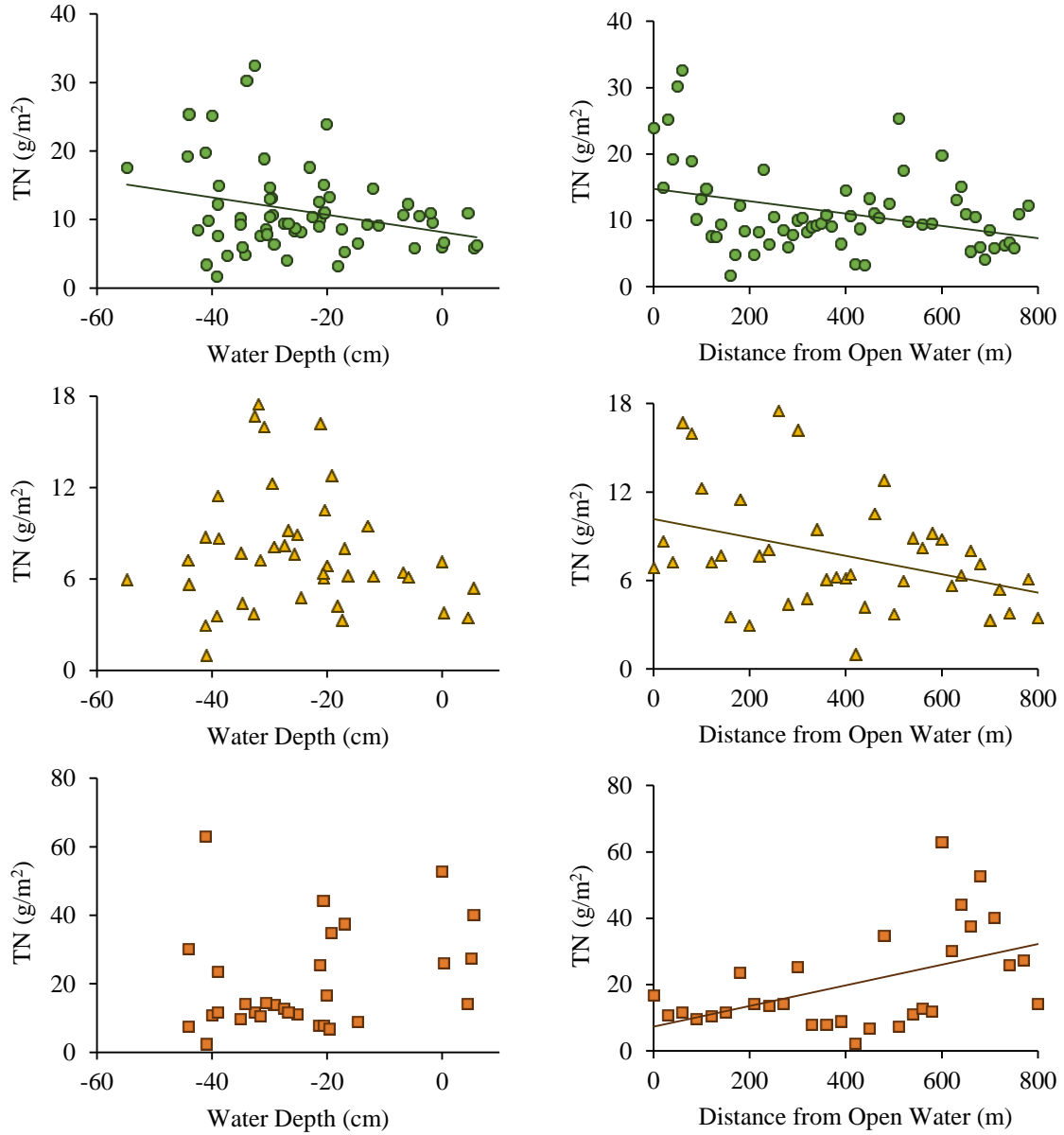


Figure 26. TN per square meter (g/m^2) in aboveground live ($n=63$) (●), aboveground dead ($n=41$) (▲), and belowground ($n=30$) (■) *Typha x glauca* tissue by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

Nutrient Interactions

The correlations between TN and TKN for aboveground live, aboveground dead, and belowground *Typha x glauca* tissues were all significant and strongly positively linear ($r(61)=0.9526$, $p<0.0001$; $r(39^*)=0.9017$, $p<0.0001$; and $r(28)=0.9486$, $p<0.0001$, respectively) (Figure 27). Slopes of all linear regression lines were similar to one.

Mean TN to TKN ratios of aboveground live and belowground *Typha x glauca* tissues were not significantly different (1.2 ± 0.1 and 1.2 ± 0.1 , respectively) ($p=0.0979$). However, they were both significantly lower than aboveground dead mean ratio (1.8 ± 0.2) ($p<0.0001$) (Table 4). Mean values were all close to one, indicating little difference in the concentrations of TKN and TN. Aboveground dead tissue ratios increased significantly with increasing depth (0.09) while ratios in aboveground live and belowground tissues were not significantly related to water depth ($p=0.59$ and $p=0.76$, respectively) (Table 4, Figure 28).

The mean TN to TP ratios of live and root tissues were not significantly different (20.4 ± 2.9 and 22.9 ± 11.3 , respectively) ($p=0.4880$). However, the dead tissue mean ratio was significantly greater than both live and root tissues (50.2 ± 14.1) ($p<0.0001$). According to Koerselman & Meuleman (1996), N:P values above 16 indicate P-limitation; all tissue types had mean ratios well above this cutoff point (Table 4). Belowground TN:TP ratios decreased significantly with increasing water depth ($p=0.003$), while the opposite relationship was observed in aboveground dead tissues ($p=0.01$). Aboveground live TN:TP ratio was unrelated to water depth or location ($p=0.19$) (Table 4, Figure 29).

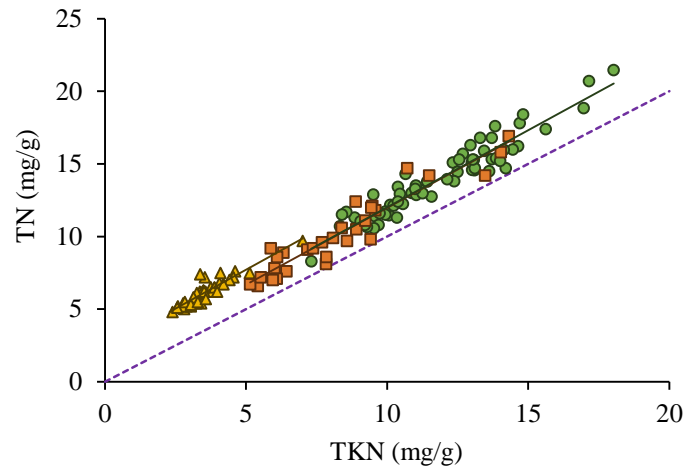


Figure 27. TN to TKN ratios of aboveground live (n=63) (●), aboveground dead (n=41) (▲), and belowground (n=30) (■) *Typha x glauca* tissue (--- 1:1 ratio) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

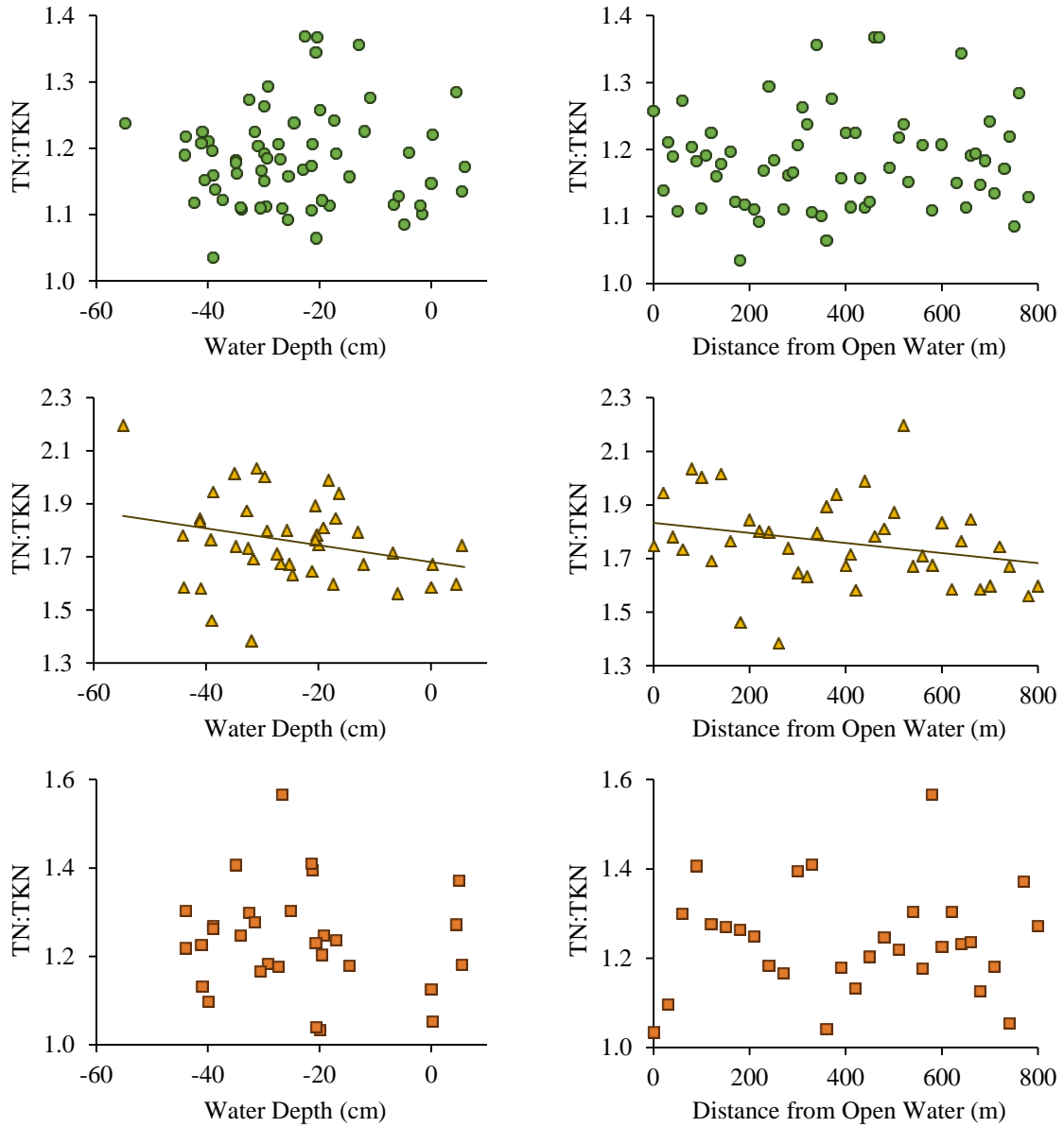


Figure 28. TN to TKN ratios in aboveground live (n=63) (●), aboveground dead (n=41) (▲), and belowground (n=30) (■) *Typha x glauca* tissue by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

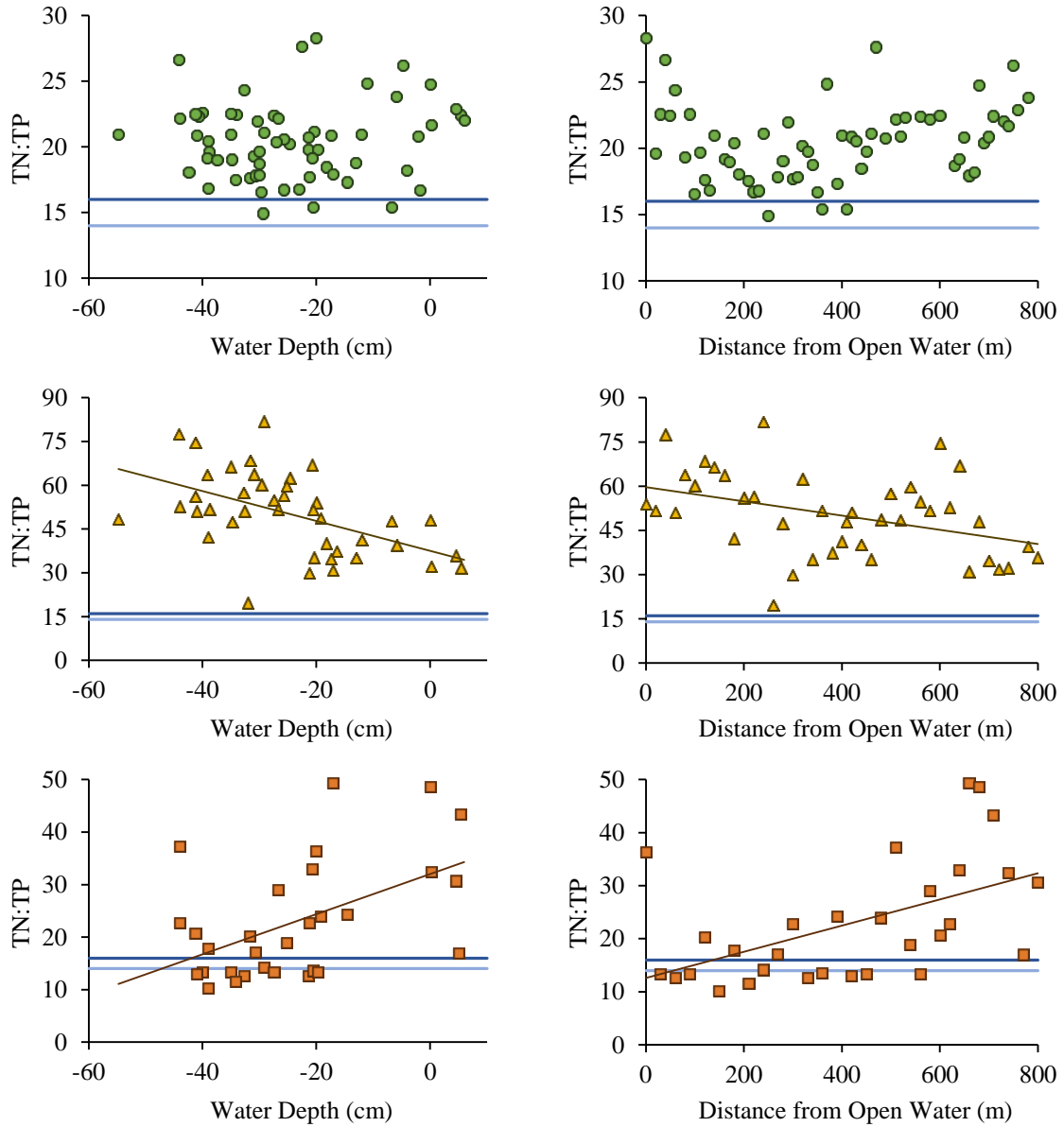


Figure 29. TN to TP ratios in aboveground live (n=63) (●), aboveground dead (n=41) (▲), and belowground (n=30) (■) *Typha x glauca* tissue by sample site water depth and location from open water (0 m) to upland (800 m) in Cell 3, Oak Hammock Marsh, Canada, 2013 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines; TN:TP ratio >16 (—) indicates P-limitation and <14 (—) indicates N-limitation as per Koerselman & Meulman, 1996).

3.4. Discussion

3.4.1. Water Depth Profile

Micro-fluctuations in the Oak Hammock Marsh transect topography / bathymetry were most likely a result of irregular accumulation of detritus and possibly muskrat activity. The significant relationship between sample site water depth and distance from open water indicates that the transect ran along a water depth gradient. Distance from open water can therefore be considered analogous to location along a saturation or water depth gradient. As the water depth measurements collected at Oak Hammock Marsh were taken over a short period of time, and therefore only reflect the water level at the time of sampling, location along a water depth gradient is a more appropriate method for analyzing the effect of water depth on growth performance and nutrient uptake.

Similar to the findings of this study, McDougal (2001) did not find emergent macrophytes growing at depths in Cell 4 greater than 50 cm. Absence of sample sites with water deeper than 55 cm may be a result of the dense *Typha* stand forming buoyant but partially-submerged mats. Observational evidence indicates that this phenomenon may have occurred at the edge of the open channel. When sample sites were first established, the *Typha* stand at open water (i.e. site 0) felt solid and well-anchored when walked upon. After repeatedly accessing the transect from site 0, the stand at that site began to feel unstable and fluid under foot, indicating that it was not anchored but a floating mat. This may explain why water depth at the edge of the open channel was only 20 cm when the channel itself was more than 75 cm deep; the *Typha* stand was floating but partially submerged.

Monodominant stands of *Typha* spp. are known to create floating mats in deep water or when water levels rise and mat buoyancy becomes sufficient to detach the mat from the substrate (Azza et al., [2006](#); Hogg & Wein, [1988](#); Krusi & Wein, [1988](#)). Mats are comprised of live belowground biomass, detritus, and mineral sediments held together by a matrix of rhizomes and roots (Azza, [2006](#)). Aerenchyma tissue in *Typha* shoots and rhizomes contribute to mat buoyancy, which increases as more biomass is produced. In older stands that have accumulated plant litter, accumulation of methane gas bubbles within organic matter produced during its anaerobic decay may further increase mat buoyancy (Hogg & Wein, [1988](#); Krusi & Wein, [1988](#)). However, *Typha* mats do not necessarily float at the water surface; the location of a mat within the water column is determined by a combination of its buoyancy and mass. Hogg and Wein ([1988](#)) found that 50-cm thick *T. x glauca* floating mats could accumulate sufficient biomass to sink to the bottom of a 90-cm basin, leaving 40 cm of standing water above the mat surface. Their study also found that mat buoyancy changed during the growing season, as new growth on the floating mats increased the amount of biomass but consequently also aerenchymous tissue, causing floating mats to become less buoyant and submerged mats to become more buoyant.

In theory, a floating mat should be able to spread and fill in open water areas, such as the open channel at OHM. However, strong winds and/or wave action may erode the edges of a floating mat, preventing it from spreading a great distance from its anchorage point and into deeper water (Azza et al., [2006](#)). Small detached clumps of *Typha* were observed along the edges of the open channel at OHM, indicating that this process occurs there.

3.4.2. Emergent Macrophyte Taxa Distribution

The spatial patterns of *Typha*, *Schoenoplectus*, and *Phragmites* presence along the transect (Figure 17) show that the zonation of emergent macrophyte species at Oak Hammock Marsh may be determined in part by relative tolerance of water depth. *T. x glauca* is capable of colonizing a wide range in water depth, though it is typically a lower marsh species, found in permanently flooded areas (Squires & van der Valk, [1992](#)). It is known to grow in areas with no standing water and thrive in water as deep as 100 cm (Boers et al., [2007](#); Seabloom et al., [1998](#); Shay & Shay, [1986](#); Squires & van der Valk, [1992](#); Waters & Shay, [1992](#)). Its parent species, *T. latifolia* and *T. angustifolia* grow in exposed mudflats to 80 cm of water and 15 to 100 cm of standing water, respectively (Grace & Wetzel, [1982](#)). At OHM, *T. x glauca* was found at all water depths along the transect, from 55 cm of standing water to 6 cm above the water table level. This confirms its tolerance for a wide range in water depth.

The presence of flowering *T. x glauca* shoots appeared unaffected by water depth, but were encountered at only just over half the sample sites. Waters & Shay ([1991](#)) postulated that low rates of flowering may be an adaptive trait for growth in wetlands, as resources normally used for flower and seed development are instead diverted to clonal expansion, a method of reproduction in which *T. x glauca* is particularly proficient (Waters & Shay, [1990](#)).

The species of *Schoenoplectus* present at OHM can tolerate a range in water depths. *Schoenoplectus tabernaemontani* (syn. *Scirpus lacustris* spp. validus) is a drawdown species (Squires & van der Valk, [1992](#)) typically found growing in wet soils and up to 60 cm of water, though its optimal range is less than 20 cm (Dabbs, [1971](#); Macaulay, [1973](#);

Seabloom et al., [1998](#)). *Schoenoplectus tabernaemontani* (syn. *Scirpus lacustris* spp. *glaucus*) is a lower marsh species and has a deeper optimal depth of 15 to 40 cm, but can tolerate wet soils and up to 1.5 m of water (Coops et al., [1996](#); Coops & van der Velde, [1996](#); Dabbs, [1971](#); Macaulay, [1973](#)). The *Schoenoplectus* spp. at OHM were found in the upper third of the transect, in depths from 44 cm of standing water to 6 cm above the water table level.

Phragmites australis (syn. *Phragmites communis* Trin) is an upper marsh species, typically found in shallow water or areas that are only seasonally flooded (Coops et al., [1996](#); Squires & van der Valk, [1992](#)). It can, however, grow in a wide range of water levels (Coops & van der Velde, [1996](#); Haslam, [1970](#); Shay & Shay, [1986](#)), from sites 100 cm above the water table to 80cm of standing water at which point it exhibits reduced growth (Coops et al., [1996](#); Shay & Shay, [1986](#)), particularly if there is competition or nutrient deficiencies (Haslam, [1970](#)). Of the three emergent macrophytes, *P. australis* had the smallest and shallowest range at OHM; it was found only in the upper 100 m of the transect, in water 6 cm deep to 6 cm above the water table level, confirming it as an upper marsh species.

While there is clear evidence of zonation along the transect saturation gradient, there were instances where *Schoenoplectus* and *Phragmites* were absent from sites located in the lower region of the transect but still within their known water depth range.

Cell 3 was in its sixth year of inundation since its drawdown in 2007. Drawdown species such as *Schoenoplectus tabernaemontani* typically disappear from a marsh if water levels are sustained for several years (Shay & Shay, [1986](#); Squires & van der Valk, [1992](#)),

which may explain its absence from sites closer to open water. Haslam (1970) found that competition limited the growth of *Phragmites* in the shallow end of its water depth range; it is therefore possible that *Phragmites* was eliminated from sites closer to open water due to the presence of the competitively superior *Typha x glauca*.

3.4.3. Biomass and Morphological Response to Water Depth

Typha x glauca aboveground live biomass at OHM ranged from 128 to 1865 g/m², and averaged 820 g/m². Boyd (1970b) found *T. latifolia* AGL biomass ranged from 728 g/m² to 2252 g/m², and averaged 951 g/m² south eastern USA locations. At two sites in Manitoba, *T. x glauca* biomass ranged from 400 g/m² to 1200 g/m² (Squires & van der Valk, 1992) and 400 g/m² to 1790 g/m² (Waters & Shay, 1992). OHM biomasses are similar to those found in other studies indicating that the conditions in OHM Cell 3 were suitable for *T. x glauca* growth at the time of sampling.

The presence of significant relationships between biomass of each tissue type and location along the water depth gradient indicates that water depth had an effect on *T. x glauca* growth performance at Oak Hammock Marsh. A full investigation including all water depths *T. x glauca* is known to colonize could not be conducted because sample sites at OHM did not exceed 55 cm of standing water, and consequently determination of an optimal depth for growth performance would not be conclusive.

Aboveground live (AGL) and dead (AGD) biomass showed positive linear relationships with increasing water depth. It is intuitive that the AGD biomass relationship to water depth reflects that of AGL, as standing dead is simply an accumulation of AGL from as many as five or six previous growing seasons. Squires & van der Valk (1992) found that

T. x glauca exhibited a curvilinear relationship with water depth, exhibiting maximum aboveground growth at depths of 45 to 75 cm, and producing less shoot tissue in shallower and deeper experimental plots. In contrast, Waters & Shay (1992) found that AGL biomass was relatively constant at depths of 25 cm to 65 cm, declined drastically at 85 cm, but peaked at the edge of the stand in 100 cm of standing water, which they partially attributed to an edge effect where access to lateral light and nutrients promotes growth. *T. domingensis* shoots had more leaves, and therefore greater AGL biomass, under low oxygen conditions and high P addition conditions (Lorenzen et al., 2001). Li et al. (2010) found that *T. domingensis* growth performance increased with addition of P. These conditions are typical of submerged wetland soils, and most likely occurred at OHM, which may explain the results of this study.

The decline in biomass at sites deeper than 85 cm found by Squires & van der Valk (1992) and Waters & Shay (1992) may be explained by increased light limitation and N-limited sediment conditions typical of deep water anoxic sediments. The process of denitrification is enhanced under anoxic conditions, while ammonification and nitrification are inhibited (Ambler et al., 2001), and this may result in N limitation. P is not likely limiting because its solubility increases under anoxic conditions, facilitating dissolution of precipitated compounds into the sediment pore water (Aldous et al., 2005; Dunne & Reddy, 2005; Young & Ross, 2001). Low biomass at sites with no standing water may be attributed to the high moisture demand of *T. x glauca* and its reduced capacity for growth in dry sites (Bedish, 1967) and limited P availability as it precipitates with metallic ions under oxic conditions (Dunne & Reddy, 2005). The deepest sites at OHM fell within the range of water depth found to produce the most biomass in the

Squires & van der Valk (1992) experiment, and before the depth that exhibited a sharp decline in the Waters & Shay (1992) study. It is therefore likely that the relationship between water depth and AGL biomass at OHM is the lower half of a curvilinear relationship, and therefore best described via a linear relationship.

In contrast to aboveground biomass, belowground (BG) *T. x glauca* biomass at OHM decreased with increasing water depth. Squires & van der Valk (1992) found that BG *T. x glauca* biomass peaked at 45 and 70 cm, and declined in deeper water. Less BG biomass in deeper water may be due to low oxygen levels and increased P availability. *T. domingensis* was found to have shorter roots, and thus less BG biomass, under low oxygen conditions, low redox potential values, and high P addition (Li et al., 2010; Lorenzen et al., 2001). Roots provide surface area for P uptake; less surface area is required under increased P availability. Low oxygen levels impede BG tissue growth and function because it is required for oxidative phosphorylation (Li et al., 2010). Other emergent macrophyte species, such as *Bolboschoenus maritimus* (syn. *Scirpus maritimus*) and *Schoenoplectus lacustris* (syn. *Scirpus lacustris*), have shown a decrease in BG biomass with increasing water depth (Coops et al., 1996; Lieffers & Shay, 1981).

T. x glauca shoot density did not change with water depth at OHM. Many studies of *Typha* species have shown that shoot density decreases with increasing water depth (Grace, 1989; Grace & Wetzel, 1982; Squires & van der Valk, 1992; Vretare et al., 2001; Waters & Shay, 1992). However, these studies all included depths in excess of 100 cm, and found that maximum density occurred from approximately 20 to 70 cm of standing water, which exceeds that of the deepest sites at OHM. *Typha x glauca* shoot density at OHM averaged 12.6 ± 5.4 shoots/m², which is at the low end of ranges seen in these

other studies of *Typha* spp. (e.g. <30 shoots/m² in Grace, 1989; 10 to 43 shoots/m² in Grace & Wetzel, 1982; 12 to 41 shoots/m² in Waters & Shay, 1992). In addition to the possibility that sites at OHM did not include sites deep enough to exhibit a response to water depth, it is possible that other variables, such as exhaustion of nutrient resources or competition for light or physical space, suppressed growth of new shoots along the entire transect, thus leading to the low and consistent density at all water depths at OHM.

T. x glauca shoot height at OHM increased with increasing water depth. This response is common among emergent macrophytes; it has been seen in *T. latifolia*, *Schoenoplectus lacustris*, *Bolboschoenus maritimus*, and *Phragmites australis* (Coops et al., 1996; Grace, 1989; Grace & Wetzel, 1982; Haslam, 1970; Lieffers & Shay, 1981) and is thought to be caused by a need for more aerial tissue capable of gas exchange and photosynthesis to compensate for increased oxygen demand in the rhizosphere and rapid attenuation of light in water that limits photosynthesis, respectively. Regarding the hybrid cattail, both Squires & van der Valk (1992) and Waters & Shay (1990) found that *T. x glauca* shoots were taller in deeper water and maintained approximately the same aerial shoot length at all water depths. They theorized that this response would ensure *T. x glauca* retained sufficient tissue above water for photosynthesis and gas exchange, an important ability for a plant rooted in hypoxic conditions. Lorenzen et al. (2001) found that *T. domingensis* leaves were tallest when high levels of P were added to experimental plots. Deep water wetland soils may have higher P availability; if this occurred at OHM, deeper sites would be expected to have taller shoots, which was the case.

Typha x glauca allocation of live biomass to aboveground tissue increased with water depth, from approximately 20% in the upland to 50% near open water. Squires & van der

Valk (1992) found that *T. x glauca* AGL biomass as a percent of total biomass ranged from 30% to 50% but did not vary significantly with depths. McNaughton (1966) found that *Typha* spp. allocated at least 50% of its biomass to root material on average. While an increase in allocation to AGL has not been documented in the hybrid cattail, Grace & Wetzel (1982) witnessed similar responses in both parental species; *T. angustifolia* responded by reducing investment in sexual structures and increasing allocation to both rhizomes and leaves, while *T. latifolia* increased the proportion of biomass allocated to leaves, largely at the expense of belowground tissue. In a separate study, Grace (1989) confirmed this response of *T. latifolia*. At OHM, the occurrence of flowering did not appear to be affected by water depth; instead allocation to BG biomass decreased with increasing water depth, indicating that its response is similar to that of the parental *T. latifolia*. In their experimental study, Lorenzen et al. (2001) concluded that *T. domingensis* increased biomass allocation to BG tissue under low P availability, which typically occur under shallow oxygenated wetland sediments. Increased biomass allocation to AGL (i.e. decreased biomass allocation to BG) in deeper sites at OHM may therefore be a response to increased P availability.

Other emergent macrophytes, such as *Carex atherodes*, *Scolochloa festucacea*, *Bolboschoenus maritimus*, *Schoenoplectus lacustris*, *Phalaris arundinaceae*, and *Phragmites australis* (Coops et al., 1996; Squires & van der Valk, 1992), are known to increase allocation to aboveground tissue in deeper water. However, Bowden (1987) points out that differences in factors such as morphology, nutrient loading, and flood-tolerance may influence above- to belowground biomass ratios, causing highly variable data.

Waters & Shay (1990, 1992) concluded that *Typha x glauca* exhibits a plastic response to water depth in its shoot density and height. They theorized that reduction in the former, if coupled by an increase in the latter, is evidence of the ability of *T. x glauca* to respond to prevailing environmental conditions by adjusting its growth at both the population and individual level, thereby maximizing use of the biological space without experiencing reduced vigour. The ability to respond with plasticity to environmental variables is key to the success of a sterile hybrid and for maintaining the dense stands that are characteristic of *T. x glauca* (Waters & Shay, 1992).

Light limitation is a concern in deeper water and the ability to increase shoot height and allocate more resources to aboveground tissue could be adaptive mechanisms to maintain productivity and ensure subsequent survivorship (Grace & Wetzel, 1982; Squires & van der Valk, 1992; Waters & Shay, 1990). However, a simultaneous increase in AGL biomass at OHM and in the Waters & Shay (1990) study indicates that this is not the case for *T. x glauca*, as insufficient light often results in reduced biomass and/or etiolated shoots (Waters & Shay, 1990). It is more likely that this response is an adaptation to the reduced condition of sediment in deeper water.

Increasing shoot height and allocation to aboveground tissue may ensure immediate survival in deep water, but a reduction in resources to rhizomes, which act as storage tissue between growing seasons and are necessary for perennials to survive from year to year, may eventually lead to eradication of the species due to inability to spread vegetatively and poor regeneration in subsequent growing seasons (Coops et al., 1996; Squires & van der Valk, 1992). This may be true for some emergent macrophytes, particularly upper marsh or drawdown species, but not so for *T. x glauca*, as evidenced

by its aggressive growth and tolerance for deeper water, traits inherited from its parent species (Waters & Shay, 1990).

In addition to coping with environmental variables, a plastic response to water depth may allow an emergent macrophyte species to avoid competitive interactions at shallower depths (Coops et al., 1996). Grace & Wetzel (1982) noted that *T. angustifolia* inhabited a wide range in water depths when *T. latifolia* was absent but did not occupy shallower sites when it was present, and concluded that the plastic response of *T. angustifolia* to water depth allowed it to migrate to deeper sites where no competitors were present. It appears that *T. x glauca* inherited this ability. However, there was very little interspecific competition at OHM, as evidenced by fewer than 15 sites that included emergent macrophyte taxa other than *Typha*, and these were restricted to only the shallowest sites. It is therefore likely that the driving force behind *Typha* spp. growth response to increasing water depth was changes in abiotic environmental variables, as previously discussed.

While *T. x glauca* AGL and BG biomass increased and decreased, respectively, total live biomass did not change significantly along the saturation gradient at OHM. This indicates that the overall productivity of *T. x glauca* was consistent along the sampled water depth range. The hybrid cattail responded to increased water depth by increasing its shoot height and allocating more resources to aboveground tissue. These results support the conclusions of Waters & Shay (1992) that *T. x glauca* responds to water depth with a plastic change in shoot height and resource allocation rather than a change in growth performance.

3.4.4. Nutrient Content Response to Water Depth

Aboveground *Typha* TP concentrations ranged from 0.19 mg/g to 2.98 mg/g, and averaged 1.5 mg/g, while TN concentrations ranged from 8.3 mg/g to 21.5 mg/g, and averaged 14.0 mg/g. These values fall within the range of concentrations of P (1 to 4 mg/g; Epstein, 1972) but were slightly below the range of N (20 to 50 mg/g; Marschner, 1995) considered adequate for mature crop plants, indicating that N may have been limiting. However, concentrations changed significantly with water depth, indicating that limiting conditions were not consistent along the water depth gradient at OHM. Aboveground live TN:TP ratios ranged from 14.93 to 28.31, and averaged 20.4. Values above 16 indicate growth under P-limiting conditions (Koerselman & Meuleman, 1996). Aboveground TN:TP values at OHM were unrelated to water depth. The disagreement between these two methods for assessing nutrient limitation is likely based in their oversimplification of analysis. Optimal tissue concentrations and TN:TP ratios likely vary between plant species, and even ecotypes. Alternatively, the conditions at Oak Hammock Marsh may be N and P co-limiting, a condition known to occur at Delta Marsh and Netley-Libau Marsh (McDougal, 2001; G. Goldsborough, personal communication, June 25, 2015).

The presence of significant relationships between location along the saturation gradient and TP, TKN, and TN at OHM indicates that water depth had an effect on nutrient concentration in *T. x glauca* tissue. As with interpretation of the growth performance data, analysis of tissue collected on the full water depth gradient *T. x glauca* is known to occupy is required before an optimal water depth for maximum plant tissue nutrient concentration can be identified. While there appear to be no studies that thoroughly

investigate the relationship between water depth and emergent macrophyte nutrient concentration, several researchers have conducted experiments on the effects of nutrient availability, redox potential, and sediment oxygen levels on growth and nutrient content (Grace, [1988](#); Li et al., [2010](#); Lorenzen et al., [2001](#); Neill, [1990](#);). These environmental factors are heavily influenced by water depth, and the results from these experiments may provide some explanation as to results of this study, as discussed below.

TP concentrations in aboveground and belowground live *Typha* tissue increased with water depth. Li et al. ([2010](#)) found that P concentration in *T. domingensis* shoot and root tissues increased with P availability, and uptake became more efficient under reduced conditions, a response they theorized was essential for growth in low redox conditions. Wetland sediments in deep water usually have negative redox potential values and are hypoxic / anoxic; dissolved inorganic P may become more available under these conditions through increased dissolution (Aldous et al., [2005](#); Dunne & Reddy, [2005](#); Young & Ross, [2001](#)). If this was the case in the deep sites at OHM, *T. x glauca* could be expected to increase its P uptake and concentration in response, which is indeed what the results of this study show.

TN concentrations increased in aboveground live tissues with increasing water depth. TKN concentrations showed the same response. N becomes increasingly unavailable with increased water depth, because the low oxygen levels and redox potential values associated with those sediments inhibit ammonification and nitrification, and enable denitrification, while the oxygenated rhizosphere still allows for ammonium assimilation by plants. However, wetland emergent macrophytes, including *T. x glauca*, oxygenate their rhizosphere, facilitating ammonification and nitrification (Brix, [1994](#)). This

increases the bioavailability of N in the sediment immediately surrounding the roots, in an otherwise N-limiting environment.

Li et al. (2010) found that N concentration in *T. domingensis* shoot and root tissues was positively correlated with P availability. This may explain the increased N concentration in *T. x glauca* AGL tissue, as its P concentration increased, reflecting increased P availability in the hypoxic / anoxic conditions of deeper water sediments. AGL biomass and height at OHM increased with depth, indicating a higher level of productivity in deeper water. Boyd & Hess (1970) found that shoot tissue nutrient concentrations, including N, were higher in productive *T. domingensis* sites than unproductive sites, which is in agreement with the results of this study.

TN and TKN concentrations in belowground tissues decreased with increasing water depth. Water depth theoretically affects the severity of N limitation and P availability (Neill, 1990). Lorenzen et al. (2001) theorized *Typha* may be able to adjust biomass and nutrient allocation in response to P availability. *T. x glauca* at OHM showed an increase in AGL biomass and allocation to AGL, and a decrease in BG biomass with increasing water depth. This may explain the decrease in BG N concentration if the changes in biomass allocation were coupled with increased allocation of N to AGL tissue with increased water depth. The concomitant decrease in belowground N concentration and increase in aboveground N concentration at OHM indicates that *T. x glauca* allocated more N to aboveground tissues at the expense of belowground tissue N concentration in response to increasing water depth.

The difference between plant tissue TN and TKN, which measures organic and ammoniacal forms of N only, can be interpreted as the amount of inorganic N stored in plant tissue. The relationship between *T. x glauca* TN and TKN at OHM was close to one and did not change with water depth. This indicates that the increase in N concentration with water depth was not a result of increased or decreased storage of N.

3.5. Conclusion

Distribution of the three emergent macrophytes at Oak Hammock Marsh revealed a subtle coenocline along the water depth gradient. *Typha x glauca* was able to occupy all water depths, while *Schoenoplectus* spp. was limited to the upper third and *Phragmites australis* limited to the shallowest sites. A steeper water depth gradient than the one studied here may be required to establish more distinct zonation of these emergent plant taxa.

Typha x glauca aboveground growth performance and nutrient content at Oak Hammock Marsh responded favourably to increasing water depth. Because *Typha* formed a monodominant stand along most of the water depth gradient, with fewer than 15 sites containing other taxa, it is likely that changes in abiotic environmental variables associated with increasing water depth were the driving force behind the response of *Typha*. Towards deeper water, *T. x glauca* exhibited longer shoots and greater biomass allocation to aboveground tissue at the expense of belowground tissue. Overall productivity did not change, indicating that the hybrid cattail exhibits a plastic response in its morphology and biomass allocation rather than a change in growth under the stress of water depth.

In general, anaerobic deep water sediments have more bioavailable P than aerobic shallow sites. This was reflected in the increased concentrations of P in aboveground and belowground tissue. Increased concentration of N is concomitant with increasing P availability, which occurred in the aboveground live tissue. Belowground tissue N concentration decreased in deeper water, possibly because allocation to aboveground tissue increased with water depth.

The apparent relationship between water depth and *T. x glauca* tissue nutrient concentration needs further study. Does this relationship exist in other emergent macrophyte species? Is there an optimal depth for maximum nutrient concentration? The answer to this last question has particularly important relevance to water management strategies of constructed wetlands, especially where emergent macrophyte standing crop is to be harvested in order to remove nutrients from the system.

Consider the following hypothetical example: a monotypic stand of *T. x glauca* in a constructed wetland has a maximum AGL tissue P concentration of 2 g/m², which occurs at depths of 30 cm and 60 cm. From a management perspective, either depth will provide optimal conditions for P removal. If standing crop is to be harvested and used, it is important to know if the sites differ in tissue nutrient concentration and biomass. Suppose the stand in 30 cm of water produces half the biomass at twice the tissue P concentration than the stand in 60 cm. A depth of 60 cm would be optimal if harvested standing crop is to be used as a biofuel as it produces more biomass. But a depth of 30 cm would be optimal if harvested standing crop was to be processed into a fertilizer, as less biomass requires less processing. Unfortunately, this study did not include a wide enough range in

water depth to determine an optimal depth for biomass and nutrient concentration. Further studies into this relationship should include sites in excess of 100 cm.

CHAPTER 4 – Effect of Water Depth and Hydroperiod on Emergent Macrophyte Biomass and Nutrient Content in Constructed Wetlands in Delta Marsh, Manitoba

4.1. Introduction

Emergent macrophytes are key components of prairie marsh ecosystems and integral to many of the services that give these wetlands value. One such service is the ability of wetlands to filter and sequester excess nutrients, chemicals, and other pollutants from the water flowing through them (Bowden, [1987](#); Boyd, [1970b](#); Engelhardt & Ritchie, [2001](#); Fink & Mitsch, [2007](#); Johnston, [1991](#); Matamoros et al., [2007](#); Tiner, [1984](#); Yang et al., [2008](#)). This ability has become increasingly important as nutrient-overloading, particularly of P and N, has been associated with eutrophication of many important water bodies (Cole, [1998](#)).

In recognition of their capacity to act as natural filters, many wetlands are being conserved or restored, and over one thousand wetlands have been constructed in North America and Europe for the purpose of treating wastewater (Cole, [1998](#)). Emergent macrophytes are both directly and indirectly involved in the filtration and sequestration process (Boyd, [1970b](#); Brix, [1994](#); Davis, [1991](#); Steward, [1970](#)). Wetlands have also been restored to return lost habitat. Emergent macrophytes form a large part of the wetland habitat and food supply that is necessary for one third of Canada's species-at-risk (Ducks Unlimited Canada, [2006](#)) and many economically important species (Tiner, [1984](#)). Management of wetlands must therefore keep the health and productivity of emergent

macrophytes as a top priority. Two environmental factors that influence emergent macrophytes and can be manipulated by managers are water depth and hydroperiod.

Many have investigated the effects of water depth on emergent macrophyte biomass, morphology, population parameters, and species zonation (Boers & Zedler 2008; Boyd & Hess 1970; Coops et al. 1996; Grace 1988, 1989; Grace & Wetzel 1981, 1982; Haslam, 1970; Lieffers & Shay 1981; McNaughton, 1966; Squires & van der Valk 1992; Vretare et al., 2001; Waters & Shay, 1990, 1992).

In general, a range in water depth corresponds to peak emergent macrophyte biomass; this range differs between species and is largely determined by their morphological and physiological adaptations to growth under declining oxygen availability and related environmental variables associated with increasing water depth. Zonation along a water depth gradient results from these differences (Spence, 1982; Stewart & Kantrud, 1971). Biomass of an emergent macrophyte may be reduced in water shallower than its optimal range because of insufficient moisture (Bedish, 1967), reduced P availability, as P precipitates with metallic ions under oxic conditions (Dunne & Reddy, 2005), an increase in salinity beyond the tolerance of the emergent macrophyte as marsh waters evaporate (Squires & van der Valk, 1992), and/or interspecific competition with species better adapted to shallow-water conditions (Grace & Wetzel; 1982). In deeper water, insufficient light for photosynthesis (Squires & van der Valk, 1992; Waters & Shay, 1992), insufficient oxygen for nutrient assimilation (Ambler et al., 2001), reduced N availability, as denitrification is favoured under anoxic conditions while nitrification and ammonification are inhibited (Ambler et al., 2001) and/or interspecific competition with

species better adapted to deep-water conditions (Grace & Wetzel; 1982) may reduce biomass of an emergent macrophyte.

Increasing prevalence of human activities that alter wetland hydrology has inspired much research on how hydroperiod affects emergent macrophytes. Boers & Zedler (2008) found that stabilized water levels enhanced *Typha x glauca* expansion and increased its P uptake. Anderson & Mitsch (2005) found no significant difference in *T. angustifolia* N and P uptake under pulsing and steady-flow hydrological regimes. *T. x glauca* growth is adversely affected by drought (van der Valk & Davis, 1980) and prolonged flooding (van der Valk, 1994). Miller & Zedler (2003) found that reed canary grass (*Phalaris arundinacea*) and prairie cordgrass (*Spartina pectinata*) both increased their shoot to root biomass ratio when flooded, but the former produced more biomass under fluctuating water levels, while the latter produced more biomass under prolonged inundation.

Understanding how water depth and hydroperiod affect emergent macrophyte growth performance and nutrient content is essential to successful wetland conservation, restoration, and management. It is also pertinent where surface water management, such as lake level regulation for hydroelectric power, influences water levels in hydrologically connected wetlands, such as lacustrine, delta, and riparian wetlands.

The objectives of this study were to investigate how emergent macrophyte growth and nutrient uptake respond to water depth and hydroperiod in a typical North America prairie marsh, and determine what, if any, water depths maximized growth and/or nutrient content.

It was hypothesized that

- 1) The biomass and nutrient content of *Typha x glauca* will vary along a gradient of water depth in monodominant stands where its distribution is due to abiotic environmental preferences rather than interspecific competition.
- 2) *Typha x glauca* that experienced two years of drawdown will exhibit greater biomass and nutrient content than those subject to only one year, because the longer dry marsh stage will have allowed more seeds to germinate and provided higher nutrient content to marsh sediments through mineralization of organic matter accumulated during previous flooded years.

4.2. Methods

4.2.1. Site Description

Delta Marsh is a 185 km² lacustrine lagoon marsh located along the southern shores of Lake Manitoba, Canada (N50°12.485, W098°13.030) (Figure 30a). Its emergent vegetation is dominated by cattail (*Typha* spp.), bulrush (*Schoenoplectus* spp., *Bolboschoenus* spp., *Scirpus* spp.), common reed (*Phragmites australis*), and whitetop grass (*Scolochloa festucacea*) (Batt, 2000; Shay & Shay, 1986; Squires & van der Valk, 1992). Its soils are neutral to slightly alkaline mineral gleysols and regosols (Walker, 1965) with a thin layer of peat (Shay & Shay, 1986). Groundwater in Delta Marsh is moderately brackish (Batt, 2000). Temperatures range from 19.1°C to -19.8°C in July and January, respectively (Batt, 2000). The marsh receives approximately 498.6 mm of precipitation annually (Batt, 2000). Other water sources include snowmelt and agricultural runoff from the landscape to the south of the marsh.

From 1980 to 1989, Delta Marsh was the site of the Marsh Ecology Research Program (MERP), a joint endeavor between Ducks Unlimited Canada and the Delta Waterfowl Foundation to improve our understanding of prairie wetland ecology and the changes experienced during a typical wet-dry cycle (Murkin et al., [2000b](#)). The project was interdisciplinary, with seven major ecosystem components studied: hydrology, water chemistry, macrophyte productivity, macrophyte litter, algae, invertebrates, and vertebrates (Murkin et al., [2000b](#)). Objectives for each discipline are summarized by Murkin et al. ([2000a](#)).

The MERP complex consisted of ten dyked marsh cells adjacent to the sand ridge separating Delta Marsh from Lake Manitoba (Figure 30b). Dykes were equipped with stop-log control structures and electric pumps so that water levels could be manipulated (± 2 cm) and the cells made to function like linked basin marshes under the Canadian Wetland Classification System (Murkin et al., [2000b](#); NWWG, [1997](#)). Cells were approximately 150 m by 300 m and ranged from 4 to 6 hectares in enclosed area. MERP cells were subject to one of four hydroperiod treatments that differed in duration of drawdown and depth of sustained water levels (Figure 31).

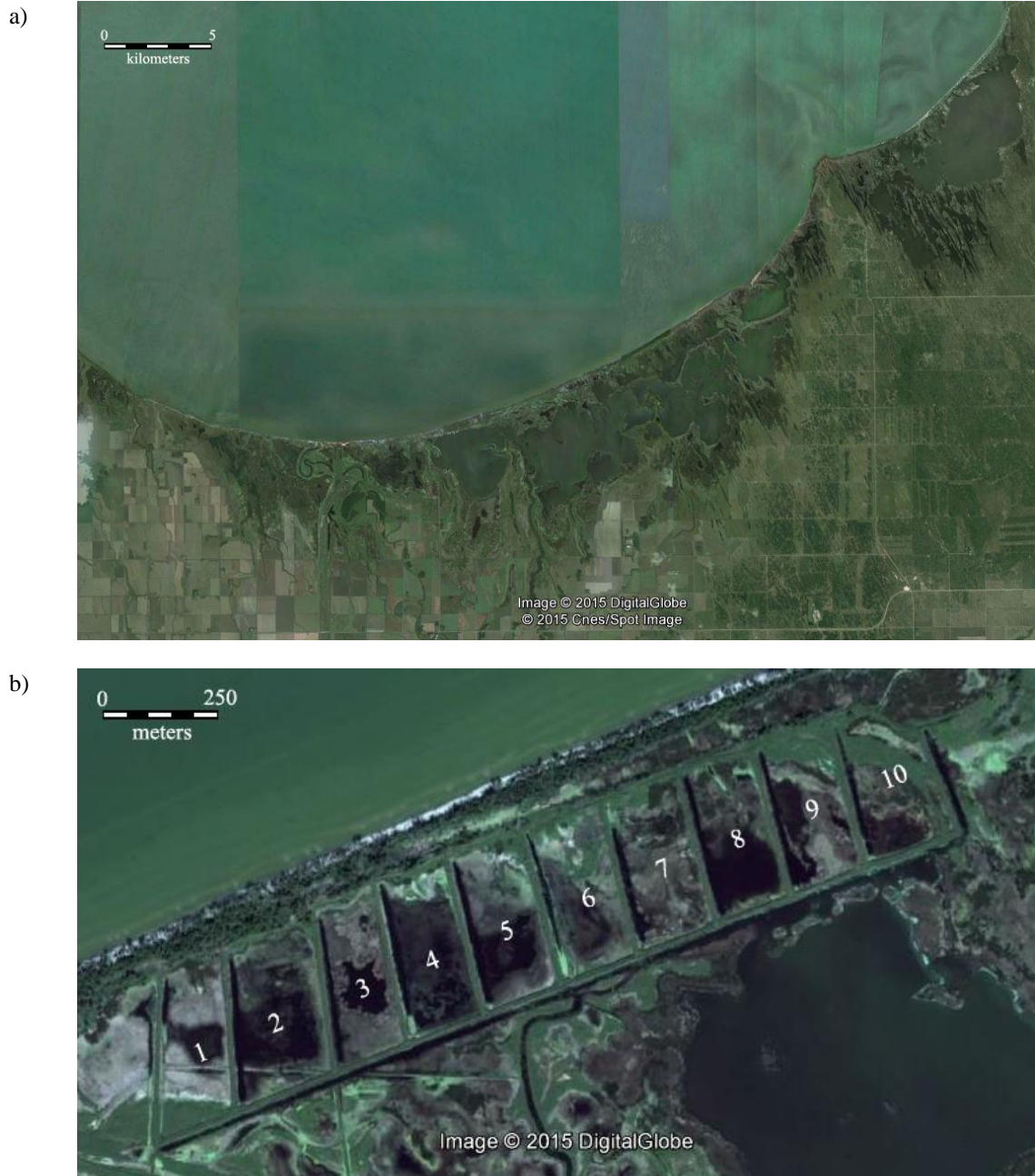


Figure 30. Delta Marsh (a) wetland and (b) Marsh Ecology Research Project experimental wetland cells (numbered one through ten, left to right), Manitoba (Source: Google™ Earth, ©DigitalGlobe, 2015, Image Date 27/8/2013).

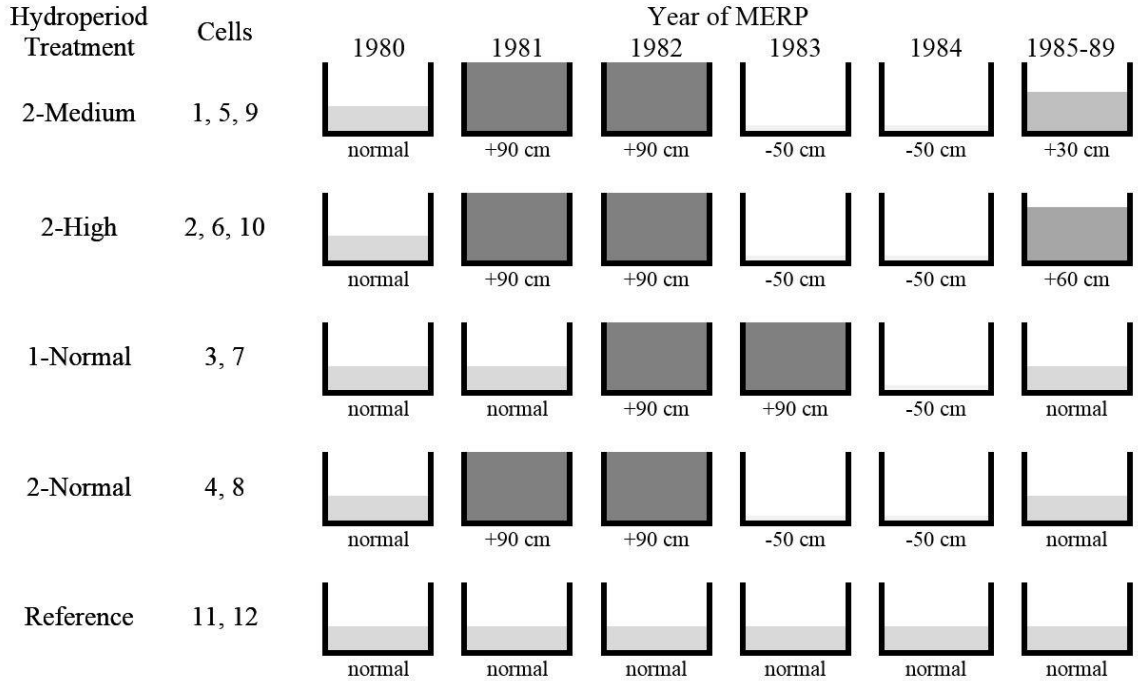


Figure 31. Marsh Ecology Research Program (MERP) cell hydroperiod treatments during baseline, deep flood and drawdown years (1980-84), and sustained water level years (1985-89) (note: water levels are given as water depth relative to normal levels (i.e. 247.5 m AMSL)).

4.2.2. Field Collection, Sample Processing, and Analysis

MERP cells were divided into ten permanently marked zones that ran parallel to the north dyke (Murkin, 1989) (Figure 32). Each zone contained one transect, or “work lane”, which ran the width of the zone, and was further divided into four subunits. New work lanes and sample site locations were determined randomly at the beginning of each sampling year; repeat locations were not allowed, macrophyte below- and aboveground sites were kept separate, and the four work lane subunits were used to ensure sampling was distributed evenly along the width of each cell (Murkin, 1989).

A detailed description of MERP vegetation sample collection and processing is provided by van der Valk (1989) and Murkin et al. (2000c). Sampling of aboveground tissue began approximately the last week of July during each year of the study, when emergent

macrophytes like *Typha* were fully grown. Four sample sites were selected randomly along the work lane in each zone, for a total of forty sites in each cell each year. Water depth was measured at each sample site; a value of 0 was assigned to sites with no standing water. Quadrats were used to delineate a standard area from which all standing vegetation was harvested and separated by species and into live versus dead subsamples. All samples were dried to constant weight at 80°C, weighed, and then ground using a Wiley mill to pass through a 0.149 mm sieve (i.e. No. 100 mesh).

Analysis of TN was conducted using a C/N elemental analyzer, while TP was analyzed using acid hydrolysis (M. Stainton, personal communication, November 6, 2013). Samples collected during the first five years (1980-1984) were analyzed by the Freshwater Institute, Winnipeg, while samples from stabilized water level years (1985-1989) were analyzed by Iowa State University (van der Valk, 1989). Only a random subset of vegetation samples were analyzed for nutrient content.

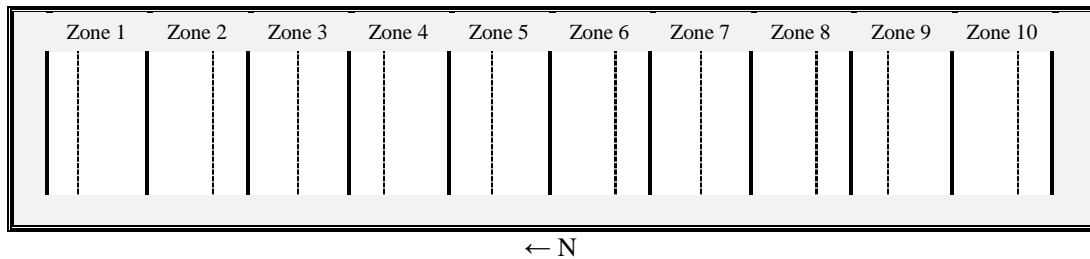


Figure 32. Schematic of a Marsh Ecology Research Program experimental wetland cell bordered by dykes (≡≡), illustrating the ten permanently marked zones (—), annually-relocated work lanes (- -), and no-sample areas (=).

4.2.3. Data Processing and Analysis

Aboveground vegetation sampling datasets were made available by Ducks Unlimited Canada through Knowledge Network for Biocomplexity (knb.ecoinformatics.org), an

international online ecological and environmental data sharing website. Four datasets were available, categorized by sampling year: 1980, 1981, 1982, and 1983-1989 (van der Valk & DUC, [2011](#)). Datasets were kept separate if their content differed from previous or subsequent years. For example, 1980 did not include sample site water depth, 1981 did not include staff gauge measurements, and 1983-1989 did not contain vegetation percent cover data. Datasets were in comma separated values (csv) file format and required conversion before analysis in Microsoft® Excel 2013 and JMP® 10. An extensible markup language (xml) file provided metadata necessary for interpretation of the datasets.

After converting all files to Excel (xls) format, columns in each dataset were organized so that all datasets included the same columns in the same order. Adding columns was necessary where measurements, such as percent cover in 1983-1989, had not been included. All four datasets were then combined to create one table that included all aboveground vegetation data for all ten years of sampling. A final column was added where observations and notes regarding the corresponding datum entry and its processing could be recorded.

Biomass data were provided as grams per sampling quadrat, and therefore required calculation of biomass per square meter. However, two quadrat sizes were used depending on which plant species were present. Quadrat size was indicated in the datasets with a numerical code, either “1” or “2”, which was interpreted using information provided in the metadata file to determine the actual quadrat area, as either 1 m² or 0.0625 m² quadrat, respectively.

Species identification was provided in the form of a six-digit numerical code which was only interpretable using information provided in the metadata file. The first two digits indicated the plant family, the second two indicated the genus, and the last two indicated the species. For example, 030101 and 030102 indicate the Cyperaceae family, *Schoenoplectus* genus, and *S. tabernaemontani* and *S. acutus* species, respectively. All data not belonging to the genera *Typha*, *Schoenoplectus*, or *Phragmites* were removed, as only major emergent macrophytes were of interest to this study. The resulting dataset was separated into three tables, one for each genus, for further processing.

Species subsample type (i.e. live versus dead) was also indicated with a numerical code in the datasets, as either “1” or “2”, which corresponded to live and dead, respectively, according to information provided in the metadata file. *Typha*, *Schoenoplectus*, and *Phragmites* datasets were further divided by live and dead subsample type, resulting in six tables.

MERP researchers separated *Typha latifolia*, *T. angustifolia*, and *T. x glauca* using morphological characters measured *in situ*. Because correct identification of the hybrid from either parent species using only morphological characters is not reliable (Kuehn & White; 1999) analyses of data were conducted at the genus level in this study. To create a dataset at the genus level, data at the species level was combined for sample sites that contained more than one species of *Typha*. Total *Typha* biomass for a sample site was calculated by summing the biomass of all *Typha* species present at that site. Similarly, *Typha* nutrient concentration was calculated using species nutrient concentration and their relative biomass at a given sample site. The same data processing was conducted for *Schoenoplectus*. Only one species of *Phragmites* was collected during MERP, so this step

in data processing was unnecessary for *Phragmites*. For an example of these calculations, see Table 5. Notes were recorded to identify entries with biomass data but had not been analyzed for nutrient content.

Sample sites did not always contain representatives of all three genera. In these cases, the original data did not contain entries for the absent genera. The result was that the six tables did not contain the same number of data entries. To standardize the tables, new entries were created such that each table contained forty sample sites per cell in each sampling year for a total of 4,800 data entries. Notes were recorded to identify entries that had been created for the purpose of standardizing the tables.

The original datasets included water depth values of zero, which were used to identify sample sites with no standing water. Because this conveyed no information regarding soil saturation, these entries and associated data were excluded from water depth analyses. This was achieved by simply deleting the zero values. Associated biomass and nutrient content data was left intact so that it would remain available for hydroperiod analyses. Notes were recorded to identify entries that had water depth values of zero in the original data. For further clarification, notes were recorded for entries that had no water depth information in the original data.

Cell, zone, and sample site number were included in the original datasets, but geographic locations for sample sites were not provided. Sample site locations changed each sampling year and were determined randomly; because the random numbers used to define their locations were not available in the online MERP datasets, annually-created

bathymetric maps for each cell could not be used to estimate water depth for those sample sites with missing values or entries of zero.

In a comparable study at Oak Hammock Marsh (see CHAPTER 3 –), *Schoenoplectus* and *Phragmites* were not found at a sufficient number of sites for analysis of the effects of water depth on emergent macrophyte growth and nutrient content. Only *Typha* occurred at a sufficient number of sites; therefore, only *Typha* data from MERP were analyzed in this study. To exclude the influence of interspecific competition, only those sample sites where *Typha* spp. was dominant were analyzed. Values used to determine dominance vary in the literature, particularly when analyzing different ecological systems. In their study of grasslands, Tarr et al. (1980) classified a species as dominant if it had a percent composition of 20% or more, while Wakeley & Lichvar (1997) declared a wetland species dominant if it accounted for 50% or more of total coverage. Because the intent in was to exclude interspecific competition, a higher cut off point was used in this study; *Typha* was considered dominant if it comprised 70% or more of the total aboveground plant biomass.

The first five years of MERP (1980-1984) were used for acclimatization and conditioning of the cells and were therefore excluded from analyses. The first post-drawdown growing season (1985) was excluded from analyses because it took until mid-August (i.e. after vegetation sampling) to flood cells to their designated water level (McKee et al., 1989). Squires & van der Valk (1992) and Coops et al. (1996) both studied the effects of water depth on emergent macrophyte growth, and after comparing differences between the results from their experimental studies and observations from natural conditions, concluded that two full growing seasons at a sustained water level did not provide enough

time for emergent macrophytes to exhibit a full response to water depth. Therefore, all data from the first and second years that experienced sustained water level over the entire growing season (1986 and 1987) were excluded from analyses. Only data from the 1988 and 1989 sampling years were analyzed in this study.

After processing *Typha* data and eliminating that which was unsuitable for analysis, it was not possible to analyze and compare all four MERP hydroperiod treatments due to low sample sizes that ranged from six to 36. Instead, data from the eight cells (1, 2, 4, 5, 6, 8, 9, and 10) that were subject to two years of drawdown in 1983-1984 (treatment DD2) were combined while data from the two cells (3 and 7) that were subject to only one year of drawdown in 1984 (treatment DD1) were combined. This created two treatments based on duration of drawdown. DD2 sample size was large enough for biomass (n=104) and nutrient (n=23) analyses, while DD1 sample size was large enough for biomass analysis (n=25) but not nutrient analysis (n=4) (see Table 6).

Biomass and nutrient concentration were used to determine mass of N and P per m². TN to TP ratios were calculated to investigate nutrient limitation as per Koerselman & Meuleman (1996). All parameters were compared to water depth to investigate what, if any, relationship existed. Tukey-Kramer analyses were conducted to determine if mean values differed between treatments. Measure of variability around mean values was estimated using standard deviation. All statistical analyses were conducted using an alpha value of 0.1. Statistical analyses were conducted using Microsoft® Excel 2013 and JMP® 10.

Table 5. Example of combining Marsh Ecology Research Program *Schoenoplectus* species biomass and nutrient content data to create one data entry at the genus level (data collected from Cell 3, Site 40, in 1989), Delta Marsh, Canada (Note: total biomass and biomass analyzed may have differed where not all species samples were analyzed for nutrient content).

Species Code	Biomass (g/m ²)		TN (mg/g)		TN (mg/m ²)
030101	28.1		11.7		328.8
030102	<u>332.0</u>	x	16.4	=	<u>5444.8</u>
<i>Schoenoplectus</i>	360.1				5773.6

<i>Schoenoplectus</i> TN	÷	Biomass Analyzed	=	<i>Schoenoplectus</i> N
5773.6 mg/m ²		360.1 g/m ²		16.0 mg/g
<i>Schoenoplectus</i> N	x	<i>Schoenoplectus</i> Biomass	=	<i>Schoenoplectus</i> N
16.0 mg/g		360.1 g/m ²		5761.6 mg/m ²

4.3. Results

Water depth at MERP sample sites dominated by *Typha* spp. in 1988-1989 ranged from 35 to 9 cm of standing water in DD1 and 87 cm to 1 cm of standing water in DD2. Biomass in DD1 decreased significantly (p=0.04) with increasing water depth, while there was no relationship between biomass and water depth in DD2 (p=0.46) (Table 6, Figure 33). Mean biomass of *Typha* spp. shoots in DD1 (547±542 g/m²) was not significantly different from DD2 mean biomass (1064±1865 g/m²) (p=0.13).

TP concentrations ranged from 1.2 mg/g to 2.3 mg/g and 0.3 mg/g to 3.2 mg/g in DD1 and DD2, respectively. TN concentrations ranged from 11.4 mg/g to 14.6 mg/g and 2.2 mg/g to 19.6 mg/g in DD1 and DD2, respectively. TN to TP ratios ranged from 12.0 to 21.9 and 7.0 to 22.9 in DD1 and DD2, respectively. Only DD2 TN concentration in tissue and TN to TP ratios were related significantly to water depth (p=0.07 and p=0.01, respectively); both decreased with increasing water depth (Table 6, Figure 34, Figure 35).

DD2 did not have significantly different mean concentrations of TP per gram of tissue (1.7 ± 0.6 mg/g) or per square meter (1.8 ± 3.6 g/m²) than DD1 ($p=0.9792$, and $p=0.5199$, respectively). Mean TN content per gram of tissue (10.7 ± 3.4 mg/g) and per square meter (8.6 ± 11.2 g/m²) in DD2 were not significantly different than those in DD1 ($p=0.3546$, $p=0.4871$, respectively). Mean TN to TP ratios did not differ significantly between DD1 (16.6 ± 4.5) and DD2 (14.5 ± 4.0) ($p=0.2508$).

Table 6. Mean (standard deviation) biomass, TP, TN, and TN to TP ratios of *Typha x glauca* shoot tissue in cells following one (DD1) or two (DD2) years of drawdown during the Marsh Ecology Research Program, Delta Marsh, Canada, 1988-89.

	Number of Years in Drawdown	Mean (SD)	Relationship to Water Depth			n
			R ²	Slope	p-value	
DD1	Biomass (g/m ²)	547 (542)	0.182	–	**0.0424	23
	TP (mg/g)	1.8 (0.5)	n/a		n/a	4
	TP (g/m ²)	0.6 (0.4)	n/a		n/a	4
	TN (mg/g)	12.7 (1.4)	n/a		n/a	4
	TN (g/m ²)	4.4 (2.4)	n/a		n/a	4
	TN:TP	16.6 (4.5)	n/a		n/a	4
	DD2	Biomass (g/m ²)	1064 (1865)	0.005		0.4553
TP (mg/g)		1.7 (0.6)	0.001		0.9010	25
TP (g/m ²)		1.8 (3.6)	0.000		0.9367	25
TN (mg/g)		10.7 (3.4)	0.139	–	*0.0660	25
TN (g/m ²)		8.6 (11.2)	0.000		0.9772	25
TN:TP		14.5 (4.0)	0.232	–	**0.0148	25

Significant relationship between measured parameter and water depth is indicate by asterisks, where ** and * indicate significance at α levels of 0.05 and 0.1, respectively. When significant, a + indicates a positive slope (value increases as water depth increases), and – indicates a negative slope (values decrease as water depth increases).

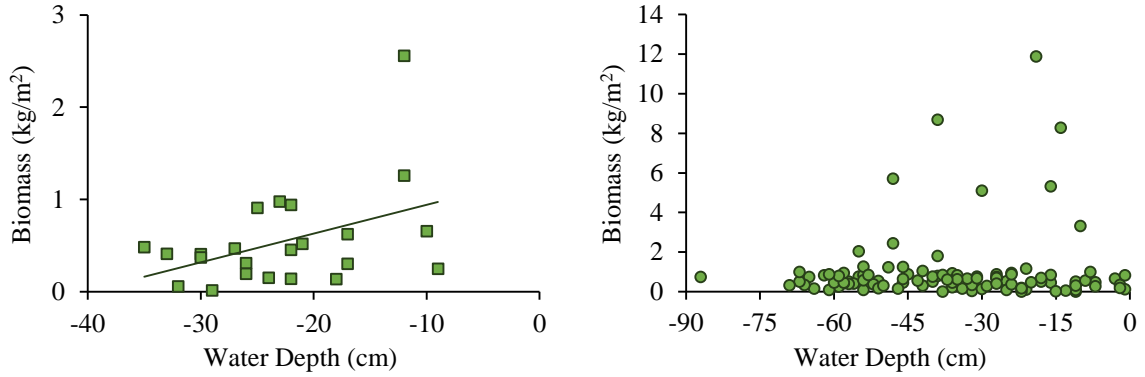


Figure 33. Biomass (kg/m²) of *Typha x glauca* collected four growing seasons after one year of drawdown (n=23) (■) and two years of drawdown (n=104) (●) in the Marsh Ecology Research Program, Delta Marsh, Canada, 1988-89, (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

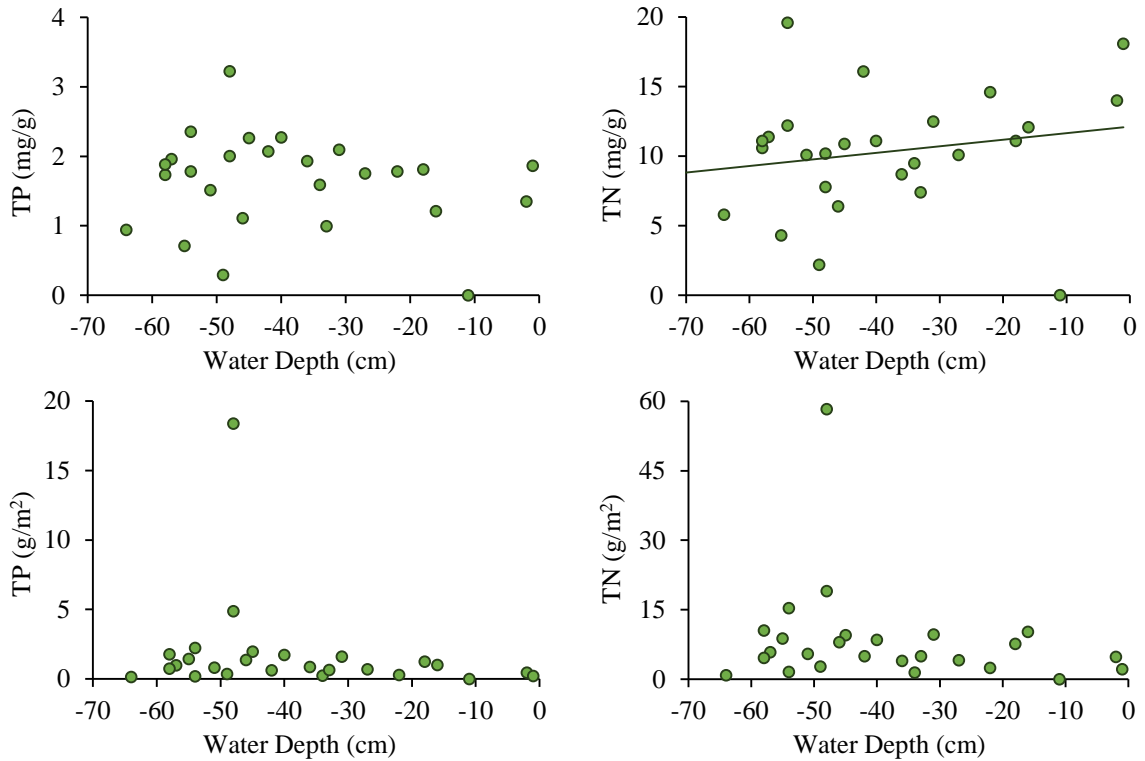


Figure 34. TP (n=25) and TN (n=25) concentration in aboveground *Typha x glauca* tissue (mg/g and g/m²) by water depth in the Marsh Ecology Research Program, Delta Marsh, Canada, 1988-89 (note: significant relationships ($\alpha=0.1$) are indicated with best-fit lines).

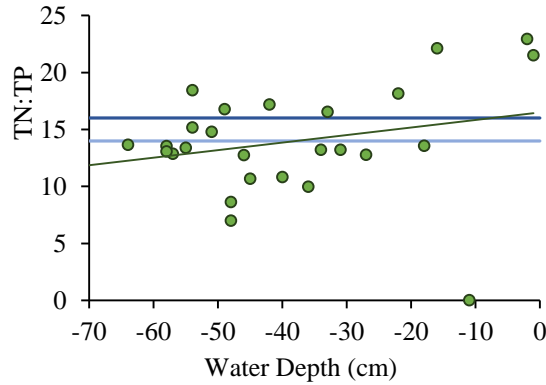


Figure 35. TN to TP ratios in aboveground *Typha x glauca* tissue (n=25) by water depth in Marsh Ecology Research Cells, Delta Marsh, Canada (note: significant relationships ($\alpha=0.1$) are indicated with a best-fit line; TN:TP ratio >16 (—) indicates P-limitation and <14 (—) indicates N-limitation as per Koerselman & Meulman, [1996](#)).

4.4. Discussion

4.4.1. Biomass Response to Water Depth and Hydroperiod

Decline in DD1 and no change in DD2 aboveground *Typha x glauca* biomass with increasing water depth was not expected. Biomass of *Typha* species have been shown to increase with increasing water depth (Squires & van der Valk, [1992](#); Waters & Shay, [1992](#)) and peak around 50 to 70 cm of water (Grace & Wetzel, [1982](#); Shay & Shay, [1986](#); Squires & van der Valk, [1992](#)). Water depths sampled in both MERP treatments did not exceed this water depth range, so biomass should have increased and a decline should not have occurred.

It is possible that the MERP cells in both treatments were in the degenerating stage of the prairie marsh wet-dry cycle at the time of sampling. While the cells were only in their fourth growing season since the dry marsh stage, the cycle can take as few as 5 years to complete (van der Valk & Davis, [1978](#)). During this stage, emergent macrophytes in deeper water experience reduced growth because they are unable to produce sufficient

aerial tissue to provide rhizomes with enough oxygen to oxygenate the rhizosphere, which in turn inhibits nutrient uptake, further reducing growth (Ball, [1990](#); van der Valk, [1994](#)). Sampling across a wide water depth range during this stage might show constant or declining emergent macrophyte biomass with increasing water depth, as depths expected to be more productive are underperforming.

Absence of a significant relationship between DD1 and DD2 mean biomass indicates that it is unlikely drawdown duration has a lasting significant effect on growth performance, especially once the degenerating stage is reached. The differences in response to water depth may partly be because the two-year drawdown treatment sampled a greater water depth range (1 to 87 cm of standing water) and had a much larger sample size (n=104) than the one-year drawdown treatment (9 to 35 cm of standing water, and n=23).

4.4.2. Nutrient Content Response to Water Depth and Hydroperiod

In both treatments, tissue P concentrations fell within the lower end of the range considered adequate for mature crop plants (1 to 4 mg/g; Epstein, [1972](#)), whereas N concentrations fell below the acceptable range (20 to 50 mg/g; Marschner, [1995](#)). This indicates that N supply may have been limiting. The range in TN:TP ratios centered around 14 to 16, the values used to determine N- or P-limiting conditions (Koerselman & Meuleman, [1996](#)). TN concentration and TN:TP ratios in the two-year drawdown treatment decreased significantly with increasing water depth, indicating that P may have been limiting in shallower sites and N became more limiting as depth increased.

Reduced aerial tissue production in deep water during the degenerating marsh stage may explain the reduction in N content, as its uptake by emergent macrophytes is highly

dependent on an oxygenated rhizosphere (Brix, [1994](#); Kozłowski, [1984](#)). P, on the other hand, is readily available under anaerobic conditions and so remained available at all depths (Bowden, [1987](#); Dunne & Reddy, [2005](#)).

Nutrient content did not differ significantly between the two treatments, indicating that effects of drawdown duration are unlikely to persist the fourth growing season or during the degenerating stage.

4.5. Conclusion

MERP wetland cells were able to progress from the dry marsh stage to a degenerating marsh within four growing seasons at sustained water levels, regardless of drawdown duration. Potential differences in emergent macrophyte aboveground biomass and nutrient content in marshes subject to different drawdown durations did not appear to last after four growing seasons, especially if the marsh had entered the degenerating marsh stage.

A recommendation regarding optimal water depth for maximum emergent macrophyte growth performance and nutrient concentration cannot be made because sampling was conducted while the marsh was in decline and over too narrow a water depth range.

During the degenerating stage, growth performance of emergent macrophytes declined in deeper water first. A reduction tissue concentration of limiting nutrients such as N may also have occurred. Therefore, it is recommended that if management of a wetland includes aboveground tissue harvest to remove nutrients from the system, the harvest be done before the marsh progresses to the degenerating stage.

Further research into effects of specific hydroperiod regimes on emergent macrophyte biomass and nutrient content are required. Does drawdown duration have an effect on the productivity or biodiversity of the marsh ecosystem? If so, does the effect last? How often does drawdown need to occur to maximize biomass or nutrient uptake? Answers to these questions are essential for developing successful wetland management strategies.

CHAPTER 5 – Synthesis and Conclusions

5.1. MERP and Oak Hammock Marsh Comparison

5.1.1. Comparison of Biomass

The response of cattail biomass to variations in water depth was inconsistent between the MERP wetlands and Oak Hammock Marsh datasets. *Typha* spp. AGL biomass at OHM increased significantly ($p=0.06$) with water depth over the range sampled (55 cm to 6 cm above the water table), while biomass in the MERP one-year drawdown treatment (DD1) decreased ($p=0.04$), and biomass in the two-year drawdown treatment (DD2) did not change ($p=0.46$) over the range sampled (35 cm to 9 cm and 87 cm to 1 cm of standing water, respectively). The different response of *Typha* spp. AGL biomass to water depth at the two study sites is most likely because OHM and MERP were in different stages of the wet-dry cycle. It was previously concluded in this study that MERP wetlands were in the degenerating stage of the prairie marsh wet-dry cycle at the time of sampling, which explains why biomass at MERP sites did not increase with water depth. The degenerating stage is characterized by a decline in emergent macrophyte biomass (van der Valk & Davis, [1978](#)), especially in areas of deeper water where exhaustion of nutrient resources is most pronounced (Coops et al., [1996](#)) and conditions such as light limitation exceed the tolerances of emergent macrophytes (Squires & van der Valk, [1992](#)). OHM was most likely in the hemi-marsh stage as it showed no signs of degeneration, such as lack of emergent macrophytes in areas of the marsh not too deep to support growth. In the hemi-marsh stage, deep water conditions such as light, nutrient, and oxygen availability have not yet become so extreme as to inhibit emergent macrophyte growth. *Typha* spp. are known to produce more AGL biomass in deeper water (Li et al., [2010](#); Lorenzen et al.,

2001; Squires & van der Valk, 1992), often because of a plastic morphological response such as leaf elongation (Squires & van der Valk, 1992; Waters & Shay, 1990) and/or increased biomass allocation to AGL tissue (Grace, 1989; Grace & Wetzel, 1982).

Mean *Typha* spp. aboveground live biomass at OHM (821 ± 393 g/m²) did not differ significantly from DD1 (547 ± 542 g/m²; $p=0.51$) or DD2 (1064 ± 1865 g/m²; $p=0.35$). MERP wetlands were degenerating marshes and should have had lower mean biomass than OHM. However, high variability in biomass at OHM and both MERP treatments makes significant differences unlikely.

5.1.2. Comparison of Nutrient Content

The response of cattail nutrient content in the OHM and MERP datasets were inconsistent. TP concentration in *Typha* spp. AGL tissue at OHM increased significantly with water depth ($p=0.006$) while TP concentration at DD2 did not change ($p=0.90$). TP in *T. domingensis* tissue has been shown to increase with increased P availability (Li et al., 2010), which occurs in deeper water where anaerobic conditions increase P dissolution and availability in soil pore water (Aldous et al., 2005; Dunne & Reddy, 2005; Young & Ross, 2001). Because OHM nutrient resources were not yet exhausted, *Typha* increased its TP concentration in deeper water, in response to greater P availability. In contrast, nutrient resources including P were most likely limited in DD2 because it was in the degenerating stage of the wet-dry cycle, as evidenced by the lack of increased biomass with increasing water depth. As a result, *Typha* TP did not increase with increasing water depth in DD2.

Typha TN concentration in aboveground live tissue at OHM increased significantly with water depth ($p=0.04$) while TN concentration at DD2 decreased ($p=0.07$). A combination of factors at OHM explains the increase in *Typha* TN concentration with water depth: nutrient availability at all depths was not yet limiting, *Typha* was able to maintain sufficient aerial tissue to oxygenate the rhizosphere for N uptake in deeper water, and P availability increased with water depth, as evidenced by the increase in AGL TP concentration in deeper water, which has been found to result in increased TN concentration in *T. domingensis* (Li et al., [2010](#)). In contrast, *Typha* at DD2 was not able to maintain sufficient aerial tissue in deeper water and the N supply was most likely exhausted, which is an instigator of the degenerating stage (Coops et al., [1996](#)), resulting in reduced TN concentration with increasing water depth.

Mean *Typha* spp. aboveground live TP concentration at OHM (1.5 ± 0.3 mg/g) was not significantly different than DD1 (1.8 ± 0.5 mg/g; $p=0.66$) or DD2 (1.7 ± 0.6 mg/g; $p=0.59$). This is not unexpected, even though OHM and MERP were in different stages of the wet-dry cycle, because P remains readily available under anoxic sediment conditions (Bowden, [1987](#); Dunne & Reddy, [2005](#)) which would have occurred in deeper sites at OHM and both MERP treatments.

Mean *Typha* spp. AGL tissue TN concentration at OHM (14.0 ± 2.6 mg/g) was significantly higher than DD2 (10.7 ± 3.4 mg/g; $p=0.006$). Because DD2 was in the degenerating stage, *Typha* was most likely unable to maintain a sufficient amount of aerial tissue to oxygenate the rhizosphere, which is required for N uptake (Brix, [1994](#); Kozłowski, [1984](#)). Also, the degenerating stage is often a result, in part, of nutrient exhaustion (Coops et al., [1996](#)). In contrast, OHM nutrient resources were not yet

limiting and *Typha* exhibited increased AGL biomass and leaf length, so was therefore able to oxygenate its rhizosphere for greater N uptake than DD2.

Mean P content per square meter of *Typha* spp. at OHM (1.2 ± 0.6 g/m²) and MERP-DD2 (1.8 ± 3.6) were not significantly different ($p=0.75$), and both were similar to values reported in the literature which ranged from 0.6 g/m² to 4.4 g/m² (Table 7). OHM mean N content (11.2 ± 6.3 g/m²) was significantly higher than at MERP-DD2 (8.6 ± 11.2 g/m²; $p=0.03$), most likely because tissue concentration was lower at DD2 than OHM. However, mean values for both sites were similar to reported values in the literature, which ranged from 3.4 g/m² to 44.2 g/m² (Table 7).

Table 7. Mean (standard deviation) *Typha* spp. N and P content (g/m²) in aboveground tissue in July – August (~ indicates values estimated from graphs; ranges indicate multiple site studies).

Species	P (g/m ²)	N (g/m ²)	Location	Source
<i>Typha</i> spp.	1.2 (0.6)	11.2 (6.3)	Oak Hammock Marsh, Canada	This study
<i>Typha</i> spp.	1.8 (3.6)	8.6 (11.2)	MERP, Delta Marsh, Canada	This study
<i>Typha</i> spp.	0.6-1.8	--	Minneapolis, Minnesota, USA	Emery & Perry, 1995
<i>T. x glauca</i>	4.4	44.2	Inlet Valley, New York, USA	Bernard & Fitz, 1979
<i>T. latifolia</i>	~0.8-1.8	~5.5-12.0	Aiken, South Carolina, USA	Boyd, 1971
<i>T. latifolia</i>	0.7	3.4	Par Pond, South Carolina, USA	Boyd, 1970a
<i>T. latifolia</i>	~3-6	~17-27	Sewage treatment wetland	Toet et al., 2015
<i>T. angustifolia</i>	1.3	12.0	Wetland mesocosm	Anderson & Mitsch, 2005
<i>T. angustifolia</i>	~1.1	~11.2	Upton Broad, Norfolk, England	Mason & Bryant, 1975
<i>T. angustifolia</i>	4.7-5.9	46.7-56.9	Lake Teganuma, Japan	Sharma et al., 2006
<i>T. domingensis</i>	~2.4	~52	Lake Burullus, Egypt	Eid et al., 2012

5.2. Evaluation of Objectives

The first objective of my study, to improve our understanding of how water depth and hydroperiod affect emergent macrophyte growth performance and nutrient content in prairie marshes, was met. *Typha* responses to increasing water depth at OHM included increased height, increased allocation to AGL biomass at the expense of BG biomass, increased TP and TN content in AGL tissue, increased TP content in BG tissue, and

decreased TN content in BG tissue. MERP wetlands progressed from a dry marsh to degenerating marsh, which is characterized by reduced emergent macrophyte biomass, in less than five years of sustained water levels.

Unfortunately, the second objective, to determine water depths and hydroperiod regimes that maximize emergent macrophyte productivity and nutrient uptake in prairie marshes, was not achieved. Sample depths at OHM did not include the full water depth range *Typha* spp. are known to occupy and therefore may not have included depths that maximize its growth and nutrient content. Wetlands of both MERP hydroperiod treatments were in the degenerating stage of the prairie marsh wet-dry cycle when sampled. This stage is characterized by a sharp decline in emergent macrophyte biomass (van der Valk & Davis, [1978](#)), most notable in deeper areas, because of insufficient light, nutrient resources, and sediment oxygen availability (Coops et al., [1996](#); Squires & van der Valk, [1992](#)), which confounds the influence of both water depth and hydroperiod on emergent macrophyte growth and nutrient content.

5.2.1. Summary of Growth Response

The overall biomass response of *Typha x glauca* to increasing water depth at Oak Hammock Marsh indicates that it exhibits a plastic morphological response to deep marsh environments; *Typha* shoots increased in height and a greater percentage of biomass was allocated to aboveground tissue with increasing water depth. This agrees with results found in other studies of *T. x glauca* (Squires & van der Valk, [1992](#); Waters & Shay, [1990](#), [1992](#)) as well as other lower marsh emergent macrophytes (Coops et al., [1996](#); Grace, [1989](#); Grace & Wetzel, [1982](#); Haslam, [1970](#); Lieffers & Shay, [1981](#); Lorenzen et al, [2001](#)).

To cope with decreased light and oxygen availability, *T. x glauca* at OHM increased its shoot height and allocated more biomass to aboveground tissue, which increases the amount of aerial tissue capable of photosynthesis and the capacity to transport oxygen to BG tissue. This occurred at the expense of belowground biomass which may have long-term consequences for vegetative reproduction in deep water, as regeneration of shoots in spring of the following growing season may be reduced.

Overall *Typha* productivity did not change along the water depth gradient at OHM, indicating that the sampled population was capable of performing equally well over the 60 cm water depth range. Aboveground biomass increased with increasing water depth at OHM, possibly in response to increased P availability (Li et al., [2010](#); Lorenzen et al., [2001](#)) while belowground biomass decreased, probably as a consequence of insufficient oxygen for necessary aerobic metabolic processes (Li et al., [2010](#)) and/or reduced need for P absorption surfaces.

MERP cells were likely in the degenerating marsh stage of the prairie marsh wet-dry cycle when sampled. As a consequence, *Typha* biomass production in deeper water was in decline, resulting in no response and reduced biomass with increasing water depth in cells subject to a two-year or one-year drawdown, respectively. It is unlikely that any potential differences in biomass due to drawdown duration persist after four growing seasons, particularly if the marsh has progressed into the degenerating stage.

5.2.2. Summary of Nutrient Content Response

TP and TN concentrations in aboveground *T. x glauca* tissue at OHM increased with increasing water depth. This is likely because P becomes more bioavailable under

increasingly anaerobic environments due to increased P dissolution (Aldous et al., [2005](#); Dunne & Reddy, [2005](#); Young & Ross, [2001](#)) and increased uptake of N is concomitant with increased uptake of P (Li et al., [2010](#)). Increasing TP concentrations in belowground tissue at OHM is also likely due to increased availability of P. The decrease in TN concentration in BG tissue at OHM may reflect limited N availability in the sediment and subsequent increasing allocation of assimilated N to aboveground tissues with increasing depth in order to maintain sufficient aerial biomass in deeper water.

Typha TN concentration decreased in aboveground tissue with increasing water depth in the MERP wetland cells, which were likely in the degenerating stage of the wet-dry cycle when sampled. Biomass declines in deeper water during this stage and, as a consequence, N becomes less available because an insufficient amount of oxygen reaches the rhizosphere due to reduced aerial tissue (Brix, [1994](#); Kozłowski, [1984](#)). P content in aboveground tissue did not change with water depth, most likely because its availability remained the same at all depths sampled. Potential differences in tissue nutrient concentration because of drawdown duration are unlikely to still be exhibited during the degenerating stage.

5.3. Management Implications

Understanding the effects of water depth and hydroperiod on emergent macrophyte growth and nutrient content are essential to designing successful water level management strategies for constructed or restored wetlands. Depending on the purpose of the wetland, maximizing emergent macrophyte growth, nutrient content, or both, may be a priority.

Sampling conditions of this study did not allow for determination of water depths that correspond to maximum emergent macrophyte biomass and nutrient content. However, the results do show that *Typha x glauca* can remain productive over a wide range in water depths, and responds positively to increases in water depth approaching 50 cm. Its ability to respond with plasticity indicates that the vigor of *T. x glauca* is not particularly vulnerable when grown in a variety of water depths. This flexibility is desirable for management purposes, as it allows some latitude in wetland design and water level management.

The results from MERP show that allowing a marsh to proceed to the degenerating stage of the wet-dry cycle negatively impacts aboveground productivity and N uptake of *Typha*. This is because nutrient resources become depleted during the degenerating stage resulting in a sharp decline in emergent macrophyte growth, especially in deeper water normally able to support growth. This could be detrimental to successful management of a wetland if nutrient removal is its main purpose. In such cases, it is recommended that sustained water levels and drawdown frequency occur such that regenerating and hemimarsh conditions are prolonged and duration of the degenerating and lake marsh stage are minimized. Unfortunately, a hydroperiod regime to achieve this end cannot be determined from the results of this study. The rapid transition from the regenerating to degenerating marsh stage at MERP under sustained water levels indicates that unintentional wetland water level stabilization, such as that experienced by coastal or riparian marshes hydrologically connected to a lake with water levels managed for hydroelectricity, may have immediately detrimental effects on emergent macrophyte productivity, and consequently on overall marsh health. This undesirable outcome will

persist so long as water levels are stabilized, as the marshes will remain in the lake marsh stage until drawdown occurs, at which point seeds can germinate and wetland macrophytes can reestablish.

Harvest of emergent macrophyte tissue from wetlands managed to remove nutrients is necessary if the nutrients are to be entirely removed from the hydrological system. Emergent macrophytes such as *Typha* spp. can contain high concentrations of N and P in their aboveground tissue (see Table 7), and thus have great potential for removing nutrients from aquatic systems, particularly in highly productive sites. However, this harvest should take place prior to the sharp decline in emergent macrophyte biomass associated with the degenerating marsh stage of the wet-dry cycle, as reduced biomass will equate to reduced nutrient removal, but also because dead tissue may leach nutrients and release them back into the aquatic system.

5.4. Future Research

Recommendations for Data Management and Metadata

Methods and data that are poorly recorded and/or lack detailed descriptions may become unusable for further analysis or unsuitable for data comparisons as time progresses. This is especially true if the researcher is unavailable for communication. Good data management practices and the use of metadata can help ensure data remain timeless.

Data management begins before any research is conducted. It starts with careful consideration of experimental design, proposed methods, quality assurance and quality control measures, and how collected data will be processed and analyzed. These aspects of data management are particularly important for innovative and/or complex research or

where there is more than one researcher. Good data management practices can help a researcher obtain results that are cohesive, precise, and accurate.

Metadata is essentially auxiliary information and/or data that describes other data and makes understanding or working with said data much easier. It may be numerical in form, such as preliminary calculations, data transformations, and generated random numbers. Metadata may also include written explanations, such as keys for interpreting data and method clarifications, like calibration details and explanations of thought processes behind modified or entirely new methods.

MERP provides an excellent example of the importance of data management and metadata. MERP experiments were long-term, very complex, and generated an enormous amount of data collected by many researchers from different disciplines of science. To provide MERP researchers with the opportunity to achieve the primary object, to further our understanding of whole-ecosystem changes experienced during the prairie marsh wet-dry cycle, proper data management was essential. MERP methods were well-conceived, having received much time and thought, but problems still occurred. For example, dykes separating experimental cells were permeable and water loss to or gain from adjacent cells complicated water budget analyses and interfered with water level control. Compilation and digitization of all available MERP data occurred more than twenty years after the experiments ended and would not have been conceivable without any metadata, even though much of it was in the form of original field data sheets and notes.

Analyses of the MERP aboveground vegetation data in this study (see CHAPTER 4 –) would have been impossible without the metadata file made available with the datasets. It

provided the necessary information to interpret various numerical codes, such as those used to identify plant species, live versus dead tissue samples, and quadrat size. However, the metadata was not complete, as many details of methods used were not recorded in the file. For example, there was no information regarding the method used to determine TN content. There are several methods for determining TN content, so this information is essential if MERP vegetation studies are to be replicated in future research, such as at OHM in this study (see CHAPTER 3 –). A now-retired MERP researcher was the only available source to clarify that TN had been analyzed using a dry combustion technique with a C/N elemental analyzer. As time passes, undocumented information such as this may become less available unless properly recorded as organized metadata.

Additional information missing from the metadata are the random numbers generated to determine sample site locations. These numbers may have been deemed unimportant once they had been used during MERP, and so not included in the metadata. However, geographic locations of sample sites are not available, possibly because they were never recorded or recorded but subsequently lost. Because both the geographic locations and random numbers were unavailable, it was impossible to determine sample site water depth using MERP topographic / bathymetric maps for those sites with no water depth values. As a consequence, many data entries were excluded from analysis in this study. Lost or unrecorded data such as this may prevent future research from being conducted using what data is available.

The following are recommendations for data management and metadata:

- 1) Document all methods, observations, and thought processes behind all decisions and record these in a cohesive manner such that they can be transcribed as metadata, especially if they are not already included in published documents as they would otherwise be unavailable.
- 2) Create metadata files as soon as possible; information is easily lost or forgotten.
- 3) Avoid the term “standard methods” as it is highly subjective, particularly where multiple methods are available; instead, fully describe or provide a published source for the methods used.
- 4) Fully explain where and why methods deviated from the cited / described methods or changed during the course of the research; future researchers may want to more fully understand how and why methods changed.
- 5) Use metadata files to make information available to future researchers so that they can fully understand the research and/or use the data; this should include information used to develop methods, conduct research, and process data, even if it seems unimportant and especially if it was not included in any published manuscripts.

Recommendations for Future Wetland Research

The effect of water depth on emergent macrophyte tissue nutrient concentration warrants further study. Determining a water depth that maximizes aboveground nutrient concentration has huge implications for wetlands designed to remove nutrients from wastewater or even non-point sources. Similarly, determining a water depth that maximizes emergent macrophyte growth performance can aid in improving wetland

design and management practices. Long-term management of wetlands requires improved understanding of the effects of hydroperiod regimes. Specifically, how often and for how long should a wetland be subject to drawdown to maximize its performance? Understanding the effects of hydroperiod manipulation on emergent macrophyte growth and nutrient content is integral to successful wetland design and management strategies.

It is recommended that future studies investigating the effect of water depth and/or hydroperiod on emergent macrophyte biomass and nutrient content include:

- 1) The full range of water depth each species present at the study site is known to occupy, in order to determine optimal water depth ranges. For example, if *Typha* spp. are present, sample sites should range from saturated soil to depths beyond its maximum depth of occurrence in natural stands in order to include areas that exceed the theoretical maximum depth and possibly include floating mats of *Typha*.
- 2) A wide variety of morphological measurements, such as number of leaves, leaf length, width, and thickness, to better investigate the plastic morphologic response of emergent macrophytes to increasing water depth.
- 3) Sediment samples analyzed for bioavailable N and P, to determine if, and at what water depths, nutrients become limiting.
- 4) Measurements of sediment redox potential values and oxygen levels at each sample site to clarify the physiological mechanisms behind emergent macrophyte responses to water depth.

Future studies investigating the influence of hydroperiod on emergent growth and nutrient content should:

- 1) Include emergent macrophyte samples collected during the hemi-marsh stage, before emergent macrophyte growth is impeded by depleted nutrient resources which occurs during the degenerating stage.
- 2) Be a long-term study, as emergent macrophytes need at least two full growing seasons to respond fully to water depth (Coops et al., [1996](#); Squires & van der Valk, [1992](#)). This could be accomplished within an MSc timeframe by sampling marshes, whose hydroperiod history is known, three years after they experienced a natural or artificial drawdown.
- 3) Not have sustained water levels well above normal or marshes may progress to the degenerating stage quickly, as they did in MERP which included wetlands subject to sustained water levels 30 cm and 60 cm above normal.

Additional questions that could be addressed in future studies include:

- 1) What abiotic and biotic environmental variables restrict emergent macrophyte growth in shallow water in the absence of interspecific competition?
- 2) Does the duration and/or frequency of drawdown affect emergent macrophyte biomass and nutrient content?
- 3) Is there a sustained water level that prolongs the hemi-marsh stage of the wet-dry cycle, in order to maximize the duration of heterogeneous habitat and resources for use by wetland fauna?

- 4) Are abiotic environmental variables of emergent macrophyte floating mats, such as nutrient availability, oxygen levels, and redox potential values, different from anchored stands? And if so, is there a difference in emergent macrophyte growth and nutrient content as a consequence?

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