

Distribution and environmental associations throughout southwestern Manitoba and southeastern Saskatchewan for the cattail species *Typha latifolia*, and *T. angustifolia*, and
for the hybrid, *T. x glauca*

By

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A Thesis submitted to the Faculty of Graduate Studies of

The University of Manitoba

in partial fulfilment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

Winnipeg

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Acknowledgements

There are many people who have given me considerable help and support, making the completion of this thesis possible. I would like to thank Ducks Unlimited Canada and Manitoba Conservation and Water Stewardship for providing the funding and use of a field truck that made this project possible. Thank you to the University of Manitoba, Delta Marsh Field Station, and Brandon University for supplying me with the space and equipment that I required. Thank you to Friends of Delta Marsh Field Station for choosing me as the recipient of a scholarship. Thank you to all of the Delta Marsh Field Station staff and fellow students for providing such an enjoyable research experience. I would like to thank my supervisors, Dr. Gordon Goldsborough, and Dr. Terry McGonigle for their guidance, expertise, and patience. Thank you Dr. Dale Wrubleski for sharing your knowledge of Delta Marsh and for solving my many truck problems quickly. Thank you Dr. Isobel Waters for joining my committee, and for your valuable comments and insights, particularly with your past work at Delta Marsh. For your guidance and assistance with statistics, thank you Dr. Darren Gillis and Dr. Norm Kenkel. Thank you Erin Anderson for your efficient assistance in the field. Thank you Maureen Foster for your neverending help with administrative affairs. Finally, I would like to thank my family, without whose support this would not have been possible. Thank you Brad, for your patience and encouragement. For the countless hours of babysitting, thank you Barb Wasko and Diane Powell.

Abstract

Cattails (*Typha* spp.) are invasive and tend to decrease the biodiversity and area of open water of marshes, particularly where the natural hydrological cycles have been altered, as in Delta Marsh, Manitoba. Understanding the distribution of *T. latifolia* L., *T. angustifolia* L., their hybrid, *T. x glauca* Godr., and the environmental variables associated with their habitats, may give valuable insight for managing cattails. The distribution of these cattail species and hybrid were surveyed in 2011 in prairie pothole and roadside ditch marshes across southwestern Manitoba and southeastern Saskatchewan. Plants were identified by analysis of microscopic leaf-lamina margin characteristics. *T. x glauca* was most widespread, followed by *T. latifolia*, whereas *T. angustifolia* was rare and only found as far west as central Manitoba. Current understanding of the correlations between cattail invasions and their environment is conflicting and largely based on lacustrine wetland studies. A generalized linear model was developed. The model explained approximately 40% of the variation in *T. x glauca* distribution in the prairie potholes and ditches. The model included the environmental variables of sediment Olsen-P, sediment nitrate-N, water pH, litter depth, surrounding land use, and the interaction between Olsen-P and nitrate-N. Olsen-P was the most important of these variables, because its removal from the model significantly reduced the residual deviance of the model ($P=0.05$). In a survey of 13 transects throughout Delta Marsh in 2009, hybrid cattail, *T. x glauca*, was dominant, *T. angustifolia* was rare, and *T. latifolia* was absent. ANOVA linear regression ($P=0.05$) revealed that above-ground biomass was correlated with mean cattail ramet height, cattail ramet density, and standing

litter biomass. Cattail ramet density was negatively correlated with sampling date and positively correlated with standing litter biomass. Mean cattail height was correlated with fallen litter biomass. One-way ANOVA ($P=0.05$) revealed that fallen litter biomass was lowest in quadrats closer to the open water, and mean cattail height was greatest at the quadrats closest to the open water. While mean cattail height differed depending on whether the cattail stand was a hybrid monoculture or a mixed stand of *T. x glauca* and *T. angustifolia*, no other cattail population variables were correlated with stand type. As revealed by one-way ANOVA ($P=0.05$), water conductivity, sediment texture, total-N, nitrate-N, Olsen-P, and organic-C were not important variables in the distributions of *T. x glauca* or *T. angustifolia* at Delta Marsh. Therefore, managing the nutrient levels at Delta Marsh would not likely be important for limiting the distribution of the cattails at this marsh. However, reducing the P concentration in pothole and ditch marshes may limit cattails in those environments.

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Chapter 1. Introduction and Literature Review

Introduction

Cattails (*Typha* spp.) are herbaceous, rhizomatous perennials, found in wetlands as diverse as bog and fen, lacustrine marshes, prairie pothole marshes, roadside ditches, riverine marshes, tidal marshes, and wet meadows (Grace and Harrison, 1986). Cattails produce long basal leaves that can reach up to 3 m (Fig. 1.1a). The female and male inflorescences are brown spikes. The spikes are borne on the same cylindrical stalk, with the female spike positioned below the male spike (Fig. 1b) (Grace and Harrison, 1986; Flora of North America, 2013). Both the leaves and the rhizomes have substantial aerenchymous tissue, which functions in aerating the submerged roots and rhizosphere (Inoue and Tsuchiya, 2008). In general, cattails are known by the following common names: cattail, cat-o'-nine-tails, cattail flag, bulrush, reed-mace, quenouille, massette, canne, tule, and queue de rat (Flora of North America, 2013). In North America, there are three cattail species, *Typha latifolia* L., *T. angustifolia* L., and *T. domingensis* Pers., as well as the hybrid, *T. x glauca* Godr. *T. latifolia* is commonly referred to as either common cattail or broad-leaved cattail, and *T. angustifolia* is commonly referred to as narrow-leaved cattail. Because my thesis focuses on the cattails of Manitoba, Canada, and the range of *T. domingensis* is limited to southern United States and Mexico (Smith, 1967), my literature review and discussion focuses on *T. latifolia*, *T. angustifolia*, and their hybrid, *T. x glauca*.

Cattail invasiveness in wetlands has been problematic throughout North America (Galatowitsch et al., 1999), Europe (Esnault and Huon, 1985) and Asia (Kim et al., 2003; Tsyusko et al., 2005). Cattails colonize new habitats via wind and water dispersal of their numerous seeds (Krattinger, 1975). *T. latifolia* seeds are intolerant of shading (Sifton, 1959). Thus, freshly disturbed sites with exposed mud flats are required for their germination. *T. latifolia* produces an average of 222,000 seeds per plant (Yeo, 1964). Once the seeds have germinated, cattails quickly spread vegetatively through the extensive growth of their rhizomes. In a greenhouse study, one seedling was observed to spread clonally to a diameter of 3 m and produce 34 mature aerial shoots (Yeo, 1964), and *T. x glauca* has been observed spreading clonally in the Great Lakes area at 5.2 m per year (Smith, 1967) and up to 8 ha per year (Boers and Zedler, 2008). Cattails form dense monocultures, often excluding other species. There has been no evidence of self-thinning in established cattail monocultures (Dickerman and Wetzel, 1985; Waters and Shay, 1992). Therefore, once cattail stands are established and dense, they are stable, and will likely persist until there is disturbance.

Cattails form dense and highly productive monocultures that displace other wetland macrophytes, colonize open water, and decrease both biodiversity and species richness (Zedler and Kercher, 2004; Angeloni et al., 2006; Craft et al., 2007; Boers and Zedler, 2008; Olson et al., 2009). For example, above-ground biomass of *T. latifolia* reached 3.4 kg m⁻² and *T. angustifolia* reached 4.0 kg m⁻² in natural ponds in eastern Europe (Dyckyjová et al., 1971); mean above-ground biomass of *T. angustifolia* reached 1.2 kg m⁻² in Lake Ontario lacustrine wetlands (Vaccaro et al. 2009); and *T. x glauca* stands at

Delta Marsh, Manitoba, reached 1.8 kg m^{-2} (Waters and Shay, 1992). Cattails tend to decrease the area of open water and mudflats, which are both important for migratory birds (Kostecke et al., 2004). Of particular concern is the hybrid cattail, *T. x glauca*, which takes advantages of disturbances. *T. x glauca* is abundant where there have been anthropogenic disturbances, such as urban development (Frieswyck and Zedler, 2007), eutrophication (Vaccarro et al., 2009), and hydrological alterations (Galatowitsch et al., 1999; Zedler and Kercher, 2004; Boers and Zedler, 2008). However, both parental species, *T. latifolia* and *T. angustifolia* can also be invasive (Grace and Harrison, 1986; Galatowitsch et al., 1999). The relative importance and interactions of urban development, eutrophication, and hydrological alterations on cattail invasiveness and on cattail species and hybrid distribution are largely unknown.

North American *Typha* species identification

Identification of North American cattail species and their hybrid with gross external morphology alone is ambiguous, especially when hybrids may be present in a mixed population. The hybrid can appear identical to either parent or as an intermediate between the two (Hotchkiss and Dozier, 1949; Fassett and Calhoun, 1952; Smith, 1967; Marcinko-Kuehn and White, 1999; Selbo and Snow, 2004). The alternatives to using gross external morphology for identification include using microscopic internal cellular structures, and using molecular techniques such as enzyme and protein assays or genetic analysis. Several studies have revealed discrepancies between gross external morphological and cellular or molecular techniques for species identification (Lee and

Fairbrothers, 1969, 1973; Lee, 1975; Suda et al., 1977; Krattinger et al., 1979; Marcinko-Kuehn and White, 1999; McManus et al., 2002).

Morphology

Quantitative morphological characters with discrete ranges for each species are potentially useful characters for identification, because they can be analyzed statistically. Leaf-apex angle and staminate-spike length have discrete ranges for *T. latifolia* and *T. angustifolia* but have not been quantified in *T. x glauca* (Kim et al., 2003). Leaf-apex angle is measured by drawing two straight lines that run from either side of the leaf blade and connect at the leaf tip, the apex. The inside angle produced from these two lines is the leaf-apex angle. Staminate-spike length is also useful for identifying *T. domingensis* (Suda et al., 1977). The identification resolution of these two characters needs to be investigated further to assess whether they can be used to identify *T. x glauca*.

The ranges for most of the quantitative characters overlap between the species and so are accurate in species identification only when morphology exhibits the extremes of the spectra. Identification is particularly ambiguous for *T. x glauca*, whose morphology is intermediate between *T. latifolia* and *T. angustifolia* (Hotchkiss and Dozier, 1949; Fassett and Calhoun, 1952; Smith, 1967; Lee and Fairbrothers, 1969; Marcinko-Kuehn and White, 1999; Selbo and Snow, 2004). The ranges overlap across the species for shoot height, stem base width, leaf height, leaf width, leaf thickness, spike gap, pistillate-spike length and width, pistillate-flower length, pedicel length, pollen grain diameter, number of main leaf veins, number of lateral leaf veins, and number of leaf blade septa (Table

1.1) (Hotchkiss and Dozier, 1949; Fassett and Calhoun, 1952; Smith, 1967; Lee and Fairbrothers, 1969; Marcinko-Kuehn and White, 1999; Finkelstein, 2003; Kim et al., 2003; Selbo and Snow, 2004). Spike-gap length refers to the length of flowering stem that is between the staminate and pistillate spikes. Pistillate-flower length includes the lengths of the stigma, style, ovary and gynophore. All of the width measurements listed above were maximum widths. The number of leaf blade septa refers to the number of septa in a cross-section of the leaf that are visible to the naked eye as raised ridges on the surface of the leaf. Because the above-listed characters overlap, they do not accurately differentiate among *T. latifolia*, *T. angustifolia*, and *T. x glauca* (Table. 1.1). For example, the range for spike gap length is larger when morphology is the sole means of identification than when molecular markers are also used. The spike gap length of *T. latifolia* ranged from 0 to 8 cm for specimens identified by morphology (Hotchkiss and Dozier, 1949; Smith, 1967; Kim et al., 2003), but it ranged from 0 to 4 cm for specimens identified by molecular markers (Lee and Fairbrothers, 1969; Marcinko-Kuehn and White, 1999; Selbo and Snow, 2004). The differences in range for this character may be due to differences between the populations sampled. However, both the morphological and molecular marker studies have representatives across North America, which should limit discrepancies from inter-population variation. Alternatively, the discrepancies may be due to misidentification of specimens using morphology alone. Such misidentification could be due to either phenotypic variation within species or from the hybridization of two or more species.

Qualitative characters may be useful for identification, but they cannot be analyzed with statistics unless they are all-or-none traits. Some qualitative characters that may be useful for identification include shape of aborted pistil, presence of pistillate bracteoles at the base of pistillate flowers, shape and colour of staminate bracteoles, shape and colour of pistillate hairs, shape of compound pedicel, shape of stigma, and type of pollen (Table 1.2) (Hotchkiss and Dozier, 1949; Fassett and Calhoun, 1952; Smith, 1967; Lee and Fairbrothers, 1969).

In contrast to gross morphology, the phenotypic expression of microscopic characters may be influenced more by genetics than the environment and therefore may be more useful for identification. Marcinko-Kuehn and White (1999) found that stigma width was more discriminant in identification than gross morphological characters, but the ranges of this trait still overlapped for *T. x glauca* and its parent species, *T. latifolia* and *T. angustifolia*. Compound pedicel length can differentiate between *T. latifolia* and *T. angustifolia*, but differentiating either of these species from *T. x glauca* is ambiguous (Hotchkiss and Dozier, 1949; Fassett and Calhoun, 1952). Marsh (1962) found that the seed characteristics of endosperm width, embryo length, and embryo width could be used to distinguish between *T. latifolia* and *T. angustifolia*, but not the hybrid (Table. 1.1). McManus et al. (2002) found that cross-sections of the flowering stem are unique for *T. x glauca*, but not for *T. latifolia* or *T. angustifolia*, because *T. x glauca* flowering stems had thicker bands of fiber than either parent species. In rhizome cross sections of *T. angustifolia*, there is a prominent band of fibers along the outer edge of the central core, and this band of fibers is less substantial in rhizomes of *T. latifolia* and *T. x glauca*. The

histochemical properties of the leaf-lamina margin differentiate among *T. latifolia*, *T. angustifolia*, and *T. x glauca*. The four leaf-lamina characteristics useful for identifying cattails to species are: (1) the general shape of the leaf edge, recorded as one of two categories: (i) oblong, or (ii) wedge; (2) the number of vascular bundles per leaf cross section within the zone of fibers near the leaf edge; (3) the presence or absence of thickened epidermal cells above the vascular bundles; and (4) the arrangement of the mesophyll cells connecting the adaxial and abaxial leaf surfaces, recorded as one of two categories: (i) mesophyll cells arranged in I-beam formation, or (ii) mesophyll cells arranged in a loose arch (McManus et al., 2002) (Table 1.3). Further investigations into microscopic characteristics may reveal more unique characters that can be used for identifying species.

Through SSR loci analysis, Snow et al. (2010) identified that the log of the ratio of leaf width to leaf length was useful in discriminating among *T. latifolia*, *T. angustifolia*, and *T. x glauca*. Spike length, spike gap length, and stem diameter were also identified as having discriminating power. A combination of these traits may provide accurate identification.

Enzyme and Protein Assays

Electrophoretic analysis of enzyme systems and electrofocusing of pollen grain proteins have demonstrated potential as diagnostic tools for investigating variation within *Typha* species. Intraspecific variation has been found among populations of *T. angustifolia* but not for *T. latifolia* or *T. x glauca* in Algeria and France using the alcohol dehydrogenase

(ADH) enzyme assay (Esnault and Huon, 1985). This same enzyme system also demonstrated intraspecific variation for *T. latifolia*, *T. angustifolia*, and *T. x glauca* among populations but not within populations in the Northeastern United States (Lee and Fairbrothers, 1973; Lee, 1975). While some studies found no intraspecific variation for esterase (EST) (Mashburn et al., 1978; Sharitz et al., 1980; Esnault and Huon, 1985), other studies found some intraspecific variation between populations but not within populations for this enzyme system (Lee and Fairbrothers 1973; Lee 1975). In a study by Sharitz et al. (1980), the phosphoglucose isomerase (PGI) enzyme system demonstrated some interpopulation variation for *T. latifolia* but there was no evidence of intraspecific variation for *T. angustifolia*, *T. x glauca*, or *T. domingensis*. A study by Mashburn et al. (1978) found no intraspecific variation in this enzyme system for either *T. latifolia* or *T. domingensis*. Studies of the acid phosphatase (AP), glutamate dehydrogenase (GDH), glutamate oxaloacetate transaminase (GOT), glucose-6-phosphate dehydrogenase (G-6-PD), isocitrate dehydrogenase (IDH), peptidase (PEPT), 6-phosphogluconate dehydrogenase (6-PGD), and phosphoglucomutase (PGM) isozyme systems and electrofocusing of pollen grain protein assays all found no intraspecific variation for *T. latifolia*, *T. angustifolia*, *T. x glauca* or *T. domingensis* (Lee and Fairbrothers, 1973; Suda et al., 1977; Mashburn et al., 1978; Krattinger et al., 1979; Sharitz et al., 1980; Esnault and Huon, 1985) and therefore these systems have the greatest potential for identifying cattail accurately to species and hybrid. As different populations of *Typha* and different enzyme systems demonstrate varying degrees of intraspecific variation, caution must be

exercised in extrapolating conclusions from one population or from one study to *Typha* as a whole.

Electrophoretic assays of the EST and GOT enzyme systems and pollen grain protein assays have demonstrated their particular usefulness for accurate species and hybrid identification. EST and GOT enzyme assays demonstrated interspecific variation for *T. latifolia*, *T. angustifolia*, *T. x glauca*, and *T. domingensis* (Lee and Fairbrothers, 1973; Lee, 1975; Suda et al., 1977; Mashburn et al., 1978; Sharitz et al., 1980; Esnault and Huon, 1985). Electrofocusing of pollen grain protein assays of *T. latifolia*, *T. angustifolia*, and their experimental hybrids displayed unique banding patterns for each species and hybrid (Lee and Fairbrothers, 1969; Krattinger et al., 1979). The banding patterns for the AP and 6-PGD isozyme systems were unique for *T. latifolia* and *T. domingensis* (Mashburn et al., 1978; Sharitz et al., 1980), but they could not distinguish between *T. angustifolia* and *T. x glauca* (Sharitz et al., 1980). The ADH enzyme system was useful for identifying *T. angustifolia* but not for discriminating between *T. x glauca* and *T. latifolia* (Lee and Fairbrothers, 1973). Sharitz et al. (1980) found that the IDH system produced different banding patterns for all of the North American *Typha* species, but Mashburn et al. (1978) found that *T. latifolia* and *T. domingensis* had identical banding patterns for this enzyme system. Some studies found that the malate dehydrogenase (MDH) system had the same banding pattern for the North American *Typha* species (Lee and Fairbrothers, 1973; Mashburn et al., 1978; Sharitz et al., 1980), but Suda et al. (1977) found that one MDH band migrated faster in *T. latifolia* than in *T. domingensis*. Discrepancies among studies may reflect intraspecific variation between

populations or variations in methodology. The glutamate dehydrogenase (GDH), glucose-6-phosphate dehydrogenase (G-6-PD), peptidase (PEPT), and phosphoglucomutase (PGM) enzyme systems showed no interspecific variation for the *Typha* species (Lee and Fairbrothers, 1973; Mashburn et al., 1978; Sharitz et al., 1980; Esnault and Huon, 1985).

Isozyme studies tend to overestimate genetic similarity, because not all changes in genetic structure result in changes in molecular weight or charge. Therefore, not all changes in genetic structure will cause different isozymes to migrate at different rates, and they may appear as the same band on the electrophoretic gel. Two of the isozyme studies noted that different populations of the same species were distinguishable morphologically, but their isozymes were indistinguishable (Lee, 1975; Suda et al., 1977). The morphological variation between populations could be due to phenotypic plasticity. However, it is likely that the resolution of isozyme analysis is too coarse to identify all intraspecific variation, because electrophoretic studies using genetic analysis found more intraspecific variation than had been previously found using isozymes (Keane et al., 1999; Tsyusko et al., 2005; Lamote et al., 2005; Zhang et al., 2008).

Genetic analysis

Genetic analysis is an accurate method for identifying *Typha* species. Molecular markers are most useful when they differentiate between all of the *Typha* species and hybrids. Analysis of DNA microsatellites revealed both intra- and inter-specific variation for *T. latifolia* and *T. angustifolia* for populations in Ukraine, with *T. angustifolia* exhibiting more variation than *T. latifolia* (Tsyusko et al., 2005). Variable number tandem repeat

(VNTR) markers demonstrated some intraspecific variation between populations of *T. latifolia* along a 320 km transect in Kentucky and Ohio. Variation was only observed when populations were at least 39 km apart (Keane et al., 1999). DNA sequencing of the nuclear genes coding for malate synthase and phytochelatin synthase revealed interspecific but not intraspecific variation for *T. latifolia* and *T. domingensis*. The nuclear gene sequence for the metallothionein-like protein gene revealed intraspecific variation for *T. domingensis* but not for *T. latifolia* and demonstrated interspecific variation between the two *Typha* species in southern Florida (Zhang et al., 2008). Sequencing revealed interspecific variation between *T. latifolia* and *T. domingensis* for the intergenic, non-coding regions, but not for the coding regions of the chloroplast genome (Zhang et al., 2008). Zhang et al. (2008) revealed the importance of investigating both coding and noncoding regions of the genome when looking for variations in highly conserved genomes. Random amplified polymorphic DNA (RAPD) markers demonstrated interspecific variation among *T. angustifolia*, *T. latifolia*, (Selbo and Snow, 2004) and *T. x glauca*, (Marcinko-Kuehn and White, 1999) but did not reveal any intraspecific variation in Ohio (Selbo and Snow, 2004), in Massachusetts, Quebec, Ontario, and Manitoba (Marcinko-Kuehn and White, 1999). Analysis of SSR loci was useful for discriminating among *T. latifolia*, *T. angustifolia*, and *T. x glauca* in Connecticut, Maryland, Michigan, Minnesota, and New York (Snow et al., 2010). Amplified fragment length polymorphism (AFLP) markers found that *T. latifolia* populations in Belgium demonstrated no intraspecific variation, but there was variation between populations of *T. angustifolia*. This variation may be due to intraspecific

variation of *T. angustifolia*, or it may be due to the presence of a hybrid, such as *T. x glauca* (Lamote et al., 2005).

Despite their widespread use in *Typha* studies, enzyme system and genetic analyses are not always feasible. Microscopic characters such as the leaf-lamina margin characters identified by McManus et al. (2002), or the seed characters identified by Marsh (1962) are more accurate than using gross morphology. Of particular use are characters derived from vegetative tissue such as the leaf-lamina margin characters, because reliable identification in such a case is not limited to the short flowering period. More research over broad geographic ranges into diagnostic characters that are accessible and practical for researchers and wetland managers to accurately identify cattail species and hybrids is required. A combination of the log of the ratio of leaf width to leaf length, spike length, spike gap length, and stem diameter identified by Snow et al. (2010) show promise for accurate identification that is more accessible than genetic analysis or microscopy.

***T. x glauca* hybrid status and phylogeny**

While *T. latifolia* and *T. angustifolia* have been found to be mostly self-fertile (Krattinger, 1975), experimental crosses between these two species and also between *T. domingensis* have revealed that hybridization is possible (Smith, 1967). Most of the hybrid cattail in the northern range of North America that have been genetically analyzed have proven to be F₁ hybrids between *T. latifolia* and *T. angustifolia* (Marcinko-Kuehn and White, 1999; Travis et al., 2010; Kirk et al., 2011). Experimental crosses indicate that introgression would be unlikely in nature, because the F₁ hybrids are mostly sterile

(Smith, 1967). In a study in Switzerland on experimental hybrids, Krattinger (1975) found that there was very low seed set with *T. latifolia* as the maternal parent and *T. angustifolia* as the pollen donor, but that hybrids formed with no difficulty when *T. angustifolia* was the maternal parent and *T. latifolia* was the pollen donor. In Michigan, most of the introgressed individuals identified were more similar to *T. angustifolia*, but some were more similar to *T. latifolia* (Snow et al. 2010). Therefore, introgression can occur with either *T. latifolia* or *T. angustifolia*.

The flowering periods of *T. latifolia* and *T. angustifolia* overlapped for only two of the eight weeks that cattails were in flower in Ohio, reducing the chances of hybridization (Selbo and Snow, 2004). In Ontario, however, the flowering periods of *T. latifolia*, *T. angustifolia*, and *T. x glauca* overlapped for at least 12 of the 16 days that the cattails were shedding pollen (Ball and Freeland, 2013). Thus, the frequency of hybridization and introgression events may depend on locality, unless the cattails are evolving. If cattails are evolving to have longer periods of synchronous flowering, we can expect hybridization and introgression to occur more often in the future.

Within natural stands, *Typha* mainly reproduces vegetatively rather than sexually through seeds (Marsh, 1962; Smith, 1967). The cattail rhizomes grow horizontally and produce new shoots, thereby expanding the cattail's clones. Hybrids can become common through clonal expansion, and introgression becomes more likely in consequence. To date, most hybrid specimens genetically analyzed that are not of the F₁ generation are more genetically similar to *T. angustifolia* than *T. latifolia*. This indicates that most of the backcrossing of hybrids with a parent have involved *T. angustifolia* rather than *T.*

latifolia (Lee, 1975; Mashburn et al., 1978; Sharitz et al., 1980; Travis et al., 2010; Kirk et al., 2011). However, Kirk et al. (2011), also found a few introgressed individuals that were more genetically similar to *T. latifolia*, indicating that backcrosses of the hybrid with *T. latifolia* also occurs naturally. Some studies have found no evidence of hybridization or introgression in *Typha*. Using RAPD markers, Selbo and Snow (2004) found no hybrids in the Ohio population studied. No evidence of hybridization between *Typha* species in Ukraine was found with DNA microsatellite analysis (Tsyusko et al., 2005). In South Carolina, there was no evidence of introgression or hybridization between *T. latifolia* and *T. domingensis*, despite the observation of highly variable morphology (Suda et al., 1977). The variation observed in the morphology of the cattails in these studies was attributed to phenotypic plasticity and genetic variation between populations. In such populations, accurate identification of *Typha* specimens can only be achieved with molecular techniques, because the morphology of the two species overlap and morphological techniques would have erroneously identified a hybrid.

All hybrid cattails are *T. x glauca* regardless of whether they are of the F₁, F₂, or further generations. How these hybrids differ from each other needs to be investigated. The range and extent of hybridization of *T. x glauca* in North America needs to be quantified. The potential range of the hybrid is wherever the ranges of different *Typha* species overlaps, but the realized range may be less. Grace and Harrison (1986) produced range maps of *T. latifolia*, *T. angustifolia*, and *T. x glauca* in North America based on herbarium specimens, published papers, and personal observations. These range maps need to be updated because the ranges of the cattails may have changed since 1986 and

the identification method with morphological traits used by Grace and Harrison (1986) is not as accurate as identification with the micro-morphology (Marsh, 1962; McManus et al, 2002) and genetic methods (Keane et al., 1999; Lamote et al., 2005; Tsyusko et al., 2005; Zhang et al., 2008) that are available today. Genetic sampling across large geographic areas using high resolution molecular techniques such as VNTR and microsatellite markers are needed to resolve the questions of the phylogeny and range of *T. x glauca*.

Invasiveness

Whereas *T. latifolia* is native to North America, *T. angustifolia* appears to be native to Europe and colonized N. America around the same time as European settlement (Grace and Harrison, 1986). Since the mid-20th century, *T. latifolia* and *T. angustifolia* have been expanding at similar rates, and the hybrid cattail is capable of forming wherever the parent species are sympatric (Grace and Harrison, 1986; Shih and Finkelstein, 2008). *T. latifolia* is present in all of the provinces of Canada (Grace and Harrison, 1986). The range of *T. angustifolia* has expanded at least as far west as central Manitoba, and *T. x glauca* has been reported as far west as Saskatchewan (Grace and Harrison, 1986; Galatowitsch et al., 1999; Shih and Finkelstein, 2008). *T. latifolia* can be found as far north as central Alaska (Smith, 1967), whereas the most northern *T. angustifolia* specimens have been found in central Manitoba (Grace and Harrison, 1986). In eastern N. America, *T. latifolia* and *T. angustifolia* were rarely found growing within the same

wetland, but *T. x glauca* was just as likely to be found growing alongside *T. latifolia* as *T. angustifolia* (Olson et al., 2009).

The invasive nature of cattails in N. America may be partly due to the hybridization between the two species. The hybrid vigour displayed by *T. x glauca*, and admixture of the two genotypes has increased the cattail genetic variability (Ciotir et al., 2013). This increase in genetic variability may have increased both the potential cattail habitat, and the competitive ability of cattails (Ciotir et al., 2013). Phenotypic plasticity of *T. x glauca* is well documented (Marsh, 1962; Grace and Harrison, 1986; Marcinko-Kuehn and White, 1999). Increased phenotypic plasticity has been linked to the successful invasion of several hybrid species (Ward et al., 2008). This phenotypic plasticity complicates conclusions made from studies where cattail species and hybrid had been identified using gross morphology.

Environmental conditions also play an important role in the invasiveness of cattails. Alterations in hydrology, eutrophication, accumulation of deep litter layers, salinity, urbanization, and agricultural intensity have all been implicated as important factors for the encroachment of *Typha* spp. and the hybrid, as discussed below. *T. latifolia* is also resistant to the sediment disturbances caused by invasive common carp (*Cyprinus carpio*), which may give it a competitive advantage over other species in marshes that have also been invaded by this fish (Miller and Provenza, 2007).

Role of hydrology

T. x glauca dominance has been associated with altered hydrology, where naturally fluctuating water levels in lacustrine marshes have been stabilized because of the installment of flooding control structures (Galatowitsch et al., 1999; Kostecke et al., 2004; van der Valk, 2005). In the Great Lakes region, *T. latifolia* and *T. angustifolia* have been found to be more abundant in areas where the water level fluctuates, while *T. x glauca* dominates areas with stabilized water levels (Boers and Zedler, 2008). The hybrid increased clonal spread and the rate of aerial shoot production, formed longer leaves, produced more above- and below-ground biomass, and increased phosphorus uptake under stabilized water conditions compared to when grown with fluctuating water levels in a mesocosm experiment (Boers and Zedler, 2008). *Typha* spp. dominance at Delta Marsh, a large lacustrine marsh along the south shore of Lake Manitoba, has been attributed to stabilized water levels (Shay et al., 1999). Since 1961, the water level of Lake Manitoba has been regulated such that the lake levels fluctuates up to 0.3 m rather than up to 1 m, as it did historically (Lake Manitoba Regulation Review Advisory Committee, 2003). Following extensive flooding in the 1950s, the marsh was dominated by *Phragmites australis*. Since the construction of a dam that regulates lake outflow, *Typha* has encroached into open water areas and largely replaced *Phragmites*.

T. x glauca can grow and produce abundant biomass in water as deep as 100 cm, with optimal growth at 25 cm and 100 cm (Waters and Shay, 1990). In a naturally colonized pond in Michigan, Grace and Wetzel (1981) found that *T. latifolia* was restricted to water depths less than 80 cm, whereas *T. angustifolia* was found growing in water as deep as

100 cm, but *T. angustifolia* growth was optimal at 80 cm. In this mixed cattail stand, *T. latifolia* outcompeted *T. angustifolia*, such that *T. angustifolia* was restricted to the deeper water. *T. angustifolia* has greater ventilation capacity from its leaves to its rhizomes than *T. latifolia*, which may help to explain why it can tolerate deeper water than *T. latifolia* (Tornbjerg et al., 1994). *T. angustifolia* also responded to hypoxic conditions by increasing root metabolism, nutrient uptake, and growth; it also produced thicker shoots and roots, and stored greater amounts of nonstructural carbon in the rhizomes. However, *T. latifolia* did not display any of these responses (Matsui and Tsuchiya, 2006; Sharma et al., 2008). These adaptations by *T. angustifolia* enable it to tolerate deeper water than *T. latifolia*.

Distribution along the water depth gradient of *T. latifolia* and *T. angustifolia* may relate not only to their intrinsic water depth tolerances, but also to the nutrient status of their environments. *T. latifolia* displaced *T. angustifolia* at lower water levels in an oligotrophic pond (Grace and Wetzel, 1998). However, in an eutrophic lake, *T. angustifolia* displaced *T. latifolia*, except at shallow water depths (Weisner, 1993). In the Great Lakes region, there was no niche segregation based on elevation found for *T. latifolia*, *T. angustifolia*, or *T. x glauca* (McKenzie-Gopsill et al., 2012). Travis et al. (2010), however, concluded that *T. latifolia* was restricted to shallow waters in the Great Lakes region. *T. latifolia* has become rare in this region and has been largely displaced by *T. x glauca*.

Alterations in hydrology may alter sedimentation rate, which could adversely affect vegetation. Increased sedimentation rates could bury existing plants, bury seeds to depths

that would inhibit germination, and decrease the light available for plants in the water column. While seed germination and seedling survivorship of *T. x glauca* was significantly reduced at sedimentation loads as little as 0.2 cm, adult plant density, number of leaves, and litter decomposition were unaffected by sediment loads as great as 4 cm (Wang et al., 1994). Thus, mature hybrid cattails may have a competitive advantage in wetlands where sedimentation rates have increased as a result of hydrological changes.

Alteration in hydrology is an important factor in cattail dominance of lacustrine marshes, but it is not the only factor involved. In the Great Lakes region, even wetlands that have retained their historical water level fluctuations have been invaded by *T. x glauca* where there was the added pressure from urbanization (Frieswyck and Zedler, 2007), although Vaccaro (2005) found that agricultural intensity was a more important factor in *T. x glauca* distribution than urbanization. Urbanization indirectly affects wetlands through alterations in hydrology and sediment quality (Frieswyck and Zedler, 2007). Increased urbanization was associated with the conversion of wet meadows to either shrubs or emergent plants. Agriculture affects wetlands through alterations in hydrology and through nutrient enrichment, which can lead to eutrophication (Vaccaro, 2005).

Role of nutrients

The invasiveness of cattails has been linked to eutrophication, with *T. x glauca* being particularly abundant in eutrophied waters, although both species and hybrid also establish in oligotrophic marshes (Bedford et al., 1999; Farrer and Goldberg, 2009). A comprehensive literature review on N and P limitation, nutrient status and species

diversity of different types of North American freshwater wetlands performed by Bedford et al. (1999) revealed that North American marshes tend to be N-limited as indicated by soil data and wetland plant tissue N:P ratios. *Typha* spp. were associated with nutrient-rich sites, with high above-ground standing biomass, and low species diversity. While most marshes are N-limited, some are P-limited, whereas others are co-limited by N and P (Craft et al., 2007). Because the majority of marshes are N-limited, N likely has a greater role than P in the invasiveness of cattails.

Cattails are efficient at uptaking N and P and may out-compete other native wetland plant species under eutrophic conditions (Woo and Zedler, 2002). Angeloni et al. (2006) found that sediments associated with *Typha* had a 14-fold increase in ammonium, a 10-fold increase in nitrate, and a 10-fold increase in phosphate compared to nearby native plant stands. *T. x glauca* may be capable of luxury uptake of nutrients (Waters and Shay, 1990), enabling it to flourish where the availability of the nutrients fluctuates. There is some evidence that at least one native species, *Schoenoplectus tabernaemontani*, can compete with the cattail under lower nutrient conditions (Svensgouk and Mitsch, 2001). In Virginia, Bevington (2007) found no differences in the soil organic matter, total-P, or total-N between created wetlands with cattails present and with cattails absent.

Above- and below-ground *T. x glauca* biomass increased with the experimental addition of P (Boers and Zedler, 2008). Inputs of P and N increased ramet density, height and biomass of *T. x glauca*, although P had more of an effect than N on total height. In contrast, fertilizer additions had no effect on the non-cattail native species (Woo and Zedler, 2002). In a greenhouse experiment, *T. angustifolia* grown under eutrophic

conditions with high N and P additions had greater growth, higher total-N and -C content in the leaves, longer rhizomes with more buds, greater starch content in the rhizomes, and lower root density than those grown in oligotrophic conditions (Steinbachová-Vojtíšková et al., 2006). Once an upper threshold is reached, excessive nutrients become detrimental to cattail growth, because plants grown in hypertrophic conditions exhibited signs of stress such as a higher proportion of yellowing leaves and unhealthy roots and rhizomes.

A competition mesocosm experiment combined with a study on a naturally colonized wastewater wetland in Ohio demonstrated that *T. latifolia* can outcompete *Schoenoplectus tabernaemontani* when N and P are high, but that its invasion is held in check under low nutrient conditions (Svenssouk and Mitsch, 2001). The mesocosm study was followed for two years only, and belowground competition was not seen at all until the second year. In the first year, *T. latifolia* outcompeted *S. tabernaemontani* in terms of above-ground biomass when both N and P were added, but *S. tabernaemontani* was able to compete with *T. latifolia* in low nutrient conditions or when only N or P but not both were added. When *Typha* rhizomes were added to established, one-year old *S. tabernaemontani* stands under low nutrient conditions, *T. latifolia* was unable to reach its maximum potential growth. This trend was corroborated by the inverse trends of *Typha* and *S. tabernaemontani* biomass in a naturally colonized wastewater treatment wetland (Svenssouk and Mitsch, 2001). *Typha* biomass was highest at the inflow, where N and P concentrations were highest, and decreased along the nutrient gradient to where P was particularly low. *S. tabernaemontani* biomass was highest at the low end, and lowest at the high end of the nutrient gradient. *Typha* allocates its energy into its rhizomes and later

uses that energy to produce massive above-ground biomass, which shades neighbours.

This competition strategy is effective, but it takes time, because *Typha* must first accumulate, store, and then re-allocate that energy. This mesocosm study only saw evidence of below-ground competition in the second year (Svenssouk and Mitsch, 2001), suggesting that it took that long for *Typha* to accumulate and store a significant amount of energy. If the study were carried through to a third or even fourth year, it is possible that this stored energy would allow *Typha* to outcompete *S. tabernaemontani* even under low nutrient conditions.

When *T. x glauca* was present in wetlands with altered hydrology in the Great Lakes region, the non-cattail native species were reduced in quantity and quality (Zedler and Kercher, 2004). The authors attributed the success of *T. x glauca* to an increase in nutrient availability from the hydrological disturbances. The presence of *T. x glauca* is not always negative. In a greenhouse experiment where pots were seeded with native sedge meadow plants with and without the hybrid cattail, the presence of *T. x glauca* enhanced the growth of native plants when nitrate levels were higher (Green and Galatowitsch, 2001). The addition of nitrate did not affect the growth of *T. x glauca* during the seedling establishment phase. Cattails did not reach adult biomass levels during the study, and so this enhancing effect of native plants and lack of any suppressive effect may have been short-term. A longer mesocosm study is needed to fully understand how nutrient conditions affect competition between cattails and other native vegetation. Ammonia is the preferred N source of *T. latifolia*. Therefore, elevations in ammonia would be expected to enhance invasiveness (Brix et al., 2002). In a study comparing pH

and N-source preference of *T. latifolia*, Brix et al., (2002) found that at near-neutral pH *T. latifolia* had higher relative growth rates, higher tissue concentrations of P, Ca, Fe, S, Na, and B, and higher affinity and uptake of inorganic N when fed ammonia as the sole N-source rather than nitrate. At pH of 5.0 and lower, nitrate became the preferred N-source. Wetlands have waterlogged, anaerobic soil where the greatest nitrogen source is ammonia (Mitsch and Gosselink, 2000), so it would be expected that plants such as *Typha* that have evolved in wetlands would have been selected for a preference for the most prevailing N source, in this case, ammonia. A study which spanned three nutrient eco-regions in Indiana found that the presence of *Typha* spp. in wetlands that were at least 40 years old was positively correlated with surface water ammonia concentrations but not with water nitrates, phosphates, or soil N or P (Craft et al., 2007). The presence of *Typha* was also correlated with low species richness (Craft et al., 2007). In Cheboygan Marsh, a lacustrine marsh of Lake Huron, soluble nutrients in the sediment including soluble ammonium, nitrate, and phosphate, as well as soil organic matter, bacterial diversity, above-ground plant biomass, and litter were significantly greater and plant species diversity was lower in sites invaded by *T. x glauca* than in native plant zones (Angeloni et al., 2006).

Typha may be able to acquire nutrients otherwise unavailable through associations with microorganisms that fix N and mycorrhizal fungi, which accumulate P. In a Minnesota wetland, *T. latifolia* was supplemented by N supplied by free-living N-fixing diazotrophs associated with its rhizosphere (Eckardt and Biesboer, 1988). The N-fixation rate peaked in August, when the cattail flowers were maturing and producing seed. This time also

coincides with the time that stored N from the rhizomes is largely depleted. The composition of denitrifying bacteria also differed between stands invaded by *T. x glauca* and nearby native plant stands (Angeloni et al., 2006) but the implications of this are unclear. *T. latifolia* was colonized by arbuscular mycorrhizal (AM) fungi under flooded conditions in a Florida wetland, but, in the greenhouse, flooding prevented colonization by the AM fungi (Ipsilantis and Silvia, 2007). AM fungi colonization was also inhibited by high P concentrations. *T. latifolia* can be colonized by AM fungi and this association may allow *Typha* greater access to P in low P environments, thereby contributing to its invasiveness. In Idaho, other researchers have found that *T. latifolia* is colonized by AM fungi during both flooding and drawdown events and that colonization rates are positively correlated with the duration of drawdown and soil moisture (Ray and Inoue, 2005).

Nutrient supply alone is not enough to explain *Typha* encroachment. In a space-for-time observational study in Cheboygan Marsh, Tuchman et al. (2009) found that *Typha* density was positively correlated with soil organic matter, phosphate, nitrate, and ammonium. However, newly invaded stands did not differ from nearby non-invaded stands with respect to these environmental variables. *T. x glauca* colonized oligotrophic sites as well as high nutrient sites in three Great Lakes lacustrine marshes in Michigan (Farrer and Goldberg, 2009), indicating that more than nutrient status is involved in cattail invasiveness.

Many of the sites where work on cattail invasiveness has been examined have a history of hydrological disturbance as well as nutrient enrichment (Lieffers, 1983; Woo and Zedler,

2002; Zedler and Kercher, 2004; Drohan et al., 2006; Boers and Zedler, 2008), so it is not possible to separate the effects of the two factors in these cases. Increased water levels and N and P inputs appear to have facilitated the encroachment of *T. latifolia* in a marl wetland in Virginia (Drohan et al., 2006). In boreal oxbow lake wetlands in Alberta, *T. latifolia* had greater above-ground biomass and stem height at sites that were more recently flooded, had deeper water, and contained higher nutrient levels (Lieffers, 1983).

The hybrid cattail seems able to compete with native plants with its higher N accumulation and also by suppressing the native vegetation with its litter in Cheboygan Marsh (Freyman, 2008). C:N levels in *Typha x glauca* leaves have been found to be significantly lower than in native plants, because *Typha x glauca* had higher N concentration. The C:N ratio was not affected by the presence or absence of *Typha* litter, suggesting that *Typha* is not suppressed by its own litter. Percent N and C:N ratios were significantly lower in the leaves of native plants where litter was present, although carbon levels did not vary.

Apart from the negative roles associated with cattails, *Typha* and other emergent species have the positive effect of reducing sediment resuspension, and in particular P-resuspension in shallow lakes, as observed in Finland (Horppila and Nurminen, 2005). This effect may reduce the productivity of eutrophic lakes.

Typha species may be associated with different sediment types. Johnston et al. (2007), in a survey along the U.S. coast of the Great Lakes, found that *Typha x glauca* was associated with organic soils, while *T. angustifolia* was associated with clay soils. However, in Michigan, the presence of *T. latifolia*, *T. angustifolia*, and the hybrid could

not be correlated with sediment texture, pH, available calcium, potassium, or available phosphorus (Segadas-Vianna, 1951). Both ammonia-N and nitrate-N were very low in all marshes surveyed by Segadas-Vianna (1951). If the different cattail species have different associations and perhaps preferences for sediment types, then they may also differ in their responses to nutrient levels. Thorough investigation into the differences between the species is required.

Both the fertilization and survey studies demonstrate that increasing the supply of N and P can aid *Typha* in its expansion, but high nutrients are not the sole factor in cattail invasiveness. *Typha* spp. are efficient at the uptake of these nutrients and form large reserves of N, P, and C, which can later be used to produce massive biomass, thereby shading nearby species (Woo and Zedler, 2002; Angeloni et al., 2006; Freyman, 2008). Cattails are capable of luxury uptake of P and form associations with microorganisms which maximize their access to both N and P. In terms of nutrient acquisition and storage, *Typha* spp. are at an advantage over other native species, but long-term fertilization studies are needed to determine if this advantage is enough to outcompete the natives. Because most North American wetlands are N-limited, with ammonia as the main N source, ammonia uptake and subsequent N storage are likely more important than P in *Typha* expansion. The differences between the cattail species and hybrid in terms of nutrient requirements are unclear, and this is an area of research that could give valuable insight. The studies discussed above have focused on the main nutrients, N and P, and to some extent, C. Studying the effects of other macronutrients and micronutrients may offer more insight into the role that nutrition plays in *Typha* expansion.

Role of litter

The deep litter layer deposited by cattails facilitates cattail expansion by excluding other species establishment through shading (Jordan et al., 1990; Farrer and Goldberg, 2009; Vaccaro et al., 2009). Stabilized water levels may prevent the physical removal of plant litter, which then accumulates and becomes detrimental to most native species. Vaccaro (2005) found that wetlands in the Great Lakes region with stabilized water levels had deeper litter layers than wetlands with fluctuating water levels, as well as lower species diversity and higher cattail cover. Because cattails are not hindered by their own litter until the litter layer reaches a depth of at least 50 cm (Jordan et al., 1990), this deep litter layer gives them a competitive advantage over other species. Freyman (2008) found that both litter accumulation and the high nitrogen accumulation rate of *T. x glauca* facilitated the competitive displacement of native vegetation in Great Lakes lacustrine wetlands.

Larkin et al. (2012) combined field observations in Cheboygan Marsh, a Great Lakes lacustrine wetland, with a six-year mesocosm experiment that investigated the interspecific and intraspecific effects of *T. x glauca* litter, live cattails and constant water depths of 0 cm and 5 cm. Larkin et al. (2012) found that litter had the largest effect on native plants, but *Typha* was not suppressed by its own litter. Plots with live *Typha* and no litter did not alter the light penetration or soil temperature but still reduced the overall native plant biomass and community composition. Litter depth altered community composition, decreased light penetration to the soil layer, decreased soil temperature, and decreased native plant biomass. In the field, Larkin et al. (2012) found that when litter was at least 10 cm deep it was a barrier to the emergence of native wetland seeds. The

water treatments altered some species-specific biomass but did not affect the total non-cattail native species biomass. However, the experiment only investigated relatively shallow water depths ranging from saturated soil with no standing water to 5 cm deep. Cattails can thrive in water levels up to 1 m (Waters and Shay, 1992), and other emergent plant species demonstrated peak biomass production at water depths of 20 cm or deeper (Squires and van der Valk, 1992). Research is needed on how native vegetation respond to combinations of litter depth and water depth, where the water depths investigated encompass the water depth tolerance range of cattails.

Role of salinity

Greenhouse studies have determined that *T. angustifolia* is more tolerant of high salinity than *T. latifolia*, whereas *T. x glauca* displays intermediate salinity tolerance (McMillan, 1959). In wetlands within salt flats in Nebraska, over a three-year period of drier conditions and therefore greater salinity, the hybrid encroached into *T. latifolia* stands but not that of *T. angustifolia* (McMillan, 1959). Growth of *T. latifolia* in the salt flats was less vigorous, and their occurrence of flowering was greatly reduced compared to both *T. angustifolia* and *T. x glauca*. Thus, the distribution of cattail species and hybrids could be affected by differences in salinity.

T. angustifolia may have a competitive advantage over native species under high salinity conditions. Miklovic and Galatowitsch (2005) found that when salt was added at the high concentration of 1000 mg L⁻¹ NaCl to microcosm plots in a Minnesota greenhouse, there was an interaction between the effect of the salt addition and the presence of cattail

seedlings on native species biomass, but not when salt was added in low doses of 500 mg L⁻¹ NaCl or less. The effect of salinity varied for different native species, suggesting that the combined effects of salt and cattail competition would vary in the field depending on the species composition. The duration of this experiment on the effects of salinity and cattail presence on native plant species by Miklovic and Galatowitsch (2005) was short, spanning 28 weeks. The cattails did not reach maturity before harvest, and so the study may have underestimated the effects of cattail presence on native species assemblages.

Implications for wetland management

Understanding the relative importance of the different environmental and genetic factors involved in cattail invasions is important for wetland managers whose goal is to increase biodiversity and limit cattail dominance. This knowledge would enable managers to utilize their resources more efficiently. For example, if altered hydrology was the sole factor for cattail invasiveness, then re-establishing historical fluctuating water levels should be effective in restoring wetlands. However, if elevated nutrient levels combined with stabilized water levels were the cause of the cattail invasion, then a management plan that only dealt with hydrology and did not include nutrient reductions would be ineffective.

The different responses to deep water and anoxia by the different cattails is important for wetland managers who wish to use techniques that rely on cutting the live and dead stems below the water. If the cattail is able to grow fast enough to reach the surface, it can quickly reoxygenate the rhizosphere and recover. Because *T. angustifolia* is better

adapted to deep water and hypoxic conditions than *T. latifolia*, it should show greater recovery from such management techniques and may require deeper levels of flooding following cutting than *T. latifolia*. *T. x glauca* is also tolerant of deep water and anoxia, because its rhizomes are able to survive continual flooding for two years (Squires and van der Valk, 1992), and so it would likely respond similarly to *T. angustifolia* when managed through cutting and flooding. Accurate identification of cattail species and hybrid is necessary for managers to decide the depth of the flooding to apply.

Conclusions

The factors involved in cattail invasiveness are complex and interrelated. Cattails can be invasive and displace native vegetation and open water, but their presence is not necessarily indicative of low plant species diversity (Green and Galatowitsch, 2001; Bevington, 2007; Freyman, 2008) Hydrology, nutrient concentrations, salinity, litter depth, and the extent of anthropogenic disturbances are potentially important factors in the invasiveness of cattails. It is difficult to decipher the relative importance of each factor even in studies that address more than one at a time. The role played by each of these factors may vary according to the *Typha* species and hybrid involved, the geographical location, the wetland type and age, and in relation to local native plant assemblages. Modeling the current distribution of *T. latifolia*, *T. angustifolia*, and *T. x glauca*, along with the potential environmental factors is the first step in identifying what the potential causative factors at a given site. Once the factors or combinations of factors have been identified, experimental studies are required to determine whether or not the

relationships are causative. How non-cattail native species compete with cattails under different environmental conditions will also be important to understand. Because cattails are perennials with large underground reserves, long-term studies that go beyond two years are necessary to assess competition effects, and to assess the effectiveness of management techniques.

As a first step for identifying what environmental factors are correlated with the distributions of *T. latifolia*, *T. angustifolia*, and *T. x glauca*, I surveyed the cattails and their environment of the large lacustrine marsh of Delta Marsh, Manitoba. I then extended the survey of the cattail species and hybrid to prairie pothole marshes and roadside ditches across western Manitoba and into eastern Saskatchewan, because their distribution has not been detailed in the literature for this region since 1986 (Grace and Harrison, 1986). I utilized generalized linear modeling to assess whether any environmental variables or combination of variables were associated with the distribution of the *T. latifolia*, *T. angustifolia* and *T. x glauca* in this region.

Table 1.1 Comparison of quantitative traits of *Typha latifolia*, *T. angustifolia*, and *T. x glauca*, as identified through morphological or molecular techniques. From Selbo and Snow, 2004^a; Finkelstein, 2003^b; Kim et al., 2003^c; Marcinko-Kuehn and White, 1999^d; Lee and Fairbrothers, 1969^e; Smith, 1967^f; Marsh, 1962^g; Fassett and Calhoun, 1952^h; Hotchkiss and Dozier, 1949ⁱ

Characteristic	<i>T. latifolia</i>	<i>T. angustifolia</i>	<i>T. x glauca</i>
Shoot height (cm) (morph.)	126 – 151 ^c	105 – 150 ^c	---
Stem base width (mm) (morph.)	1.7 – 2.5 ^c	1.3 – 2.3 ^c	---
Leaf width (mm) (morph.)	9 – 15 ^c	5 – 9 ^c	---
Leaf width (mm) (mol.)	7.5 – 23 ^{d,e}	4.5 – 12.0 ^{d,e}	6.0 – 21.0 ^{d,e}
Leaf thickness (mm) (morph.)	1.0 – 2.0 ^c	1.0 – 2.2 ^c	---
Leaf-apex angle (degree) (morph.)	8.5 – 13.9 ^c	4.0 – 6.0 ^c	---
Number of main leaf veins (morph.)	10 – 13 ^c	8 – 12 ^c	---
Number of lateral leaf veins (morph.)	2 – 5 ^c	2 – 4 ^c	---
Number of leaf blade septa (morph.)	11 – 15 ^c	8 – 12 ^c	---
Staminate spike length (cm) (morph.)	9.0 – 12.0 ^c	17.9 – 27.7 ^c	---
Spike gap (cm) (morph.)	0 – 8 ^{c,f,i}	1 – 12 ^{c,f,i}	0 – 4 ⁱ
Spike gap (cm) (mol.)	0 – 4 ^{d,e}	0 – 12 ^{a,d,e}	0 – 4.2 ^{d,e}
Pistillate-spike length (cm) (morph.)	0 – 20.3 ^{c,i}	0.5 – 20.7 ^{c,i}	8 – 20 ⁱ
Pistillate-spike length (cm) (mol.)	8.5 – 23.0 ^{d,e}	6.9 – 30.1 ^{d,e}	10 – 28.1 ^{d,e}
Pistillate-spike width (cm) (morph.)	1.6 – 3.2 ^{c,f,i}	0.9 – 2.0 ^{c,f,i}	---
Pistillate-spike width (cm) (mol.)	1.1 – 4.1 ^{d,e}	0.6 – 2.2 ^{d,e}	0.6 – 2.5 ^{d,e}
Pistillate-flower length (stigma + style + ovary + gynophore) (mm) (morph.)	1.8 – 3 ⁱ	1.3 – 2 ⁱ	1.8 – 2.5 ⁱ
Stigma width (μm) (mol.)	7 – 15 ^d	3 – 6 ^d	5 – 8 ^d
Compound-pedicel length (mm) (morph.)	1.5 – 3.5 ⁱ	0.5 – 0.7 ⁱ	0.6 – 1.2 ⁱ
Pollen grain diameter (μm) (morph.)	6.4 – 11.0 ^c	1.7 – 6.9 ^{b,c}	1.6 – 3.1 ^b
Endosperm width (mm) (morph.)	0.052 – 0.065 ^g	0.045 – 0.059 ^g	0.056 – 0.083 ^g
Embryo length (mm) (morph.)	0.971 – 1.325 ^g	0.716 – 0.902 ^g	1.060 – 1.225 ^g
Embryo width (mm) (morph.)	0.149 – 0.191 ^g	0.095 – 0.143 ^g	0.148 – 0.182 ^g

Table 1.2 Comparison of qualitative traits of *Typha latifolia*, *T. angustifolia*, and *T. x glauca*, as identified through morphological or molecular techniques. From Selbo and Snow, 2004^a; Finkelstein, 2003^b; Kim et al., 2003^c; Marcinko-Kuehn and White, 1999^d; Lee and Fairbrothers, 1969^e; Smith, 1967^f; Marsh, 1962^g; Fassett and Calhoun, 1952^h; Hotchkiss and Dozier, 1949ⁱ

Characteristic	<i>T. latifolia</i>	<i>T. angustifolia</i>	<i>T. x glauca</i>
Pollen type (monads / dyads / triads / tetrads) (morph.)	tetrads ^f	monads, dyads ^{b,f}	monads, dyads, triads, tetrads ^b
Pollen type (monads / dyads / triads / tetrads) (mol.)	tetrads ^{a,e}	monads ^{a,e}	monads, dyads, triads, tetrads ^e
Aborted-pistil shape (morph.)	club- or pear-shaped, light buff, sharply defined central space with two locules in cross-section ^h	flattened and wider at the tip; dark buff with reddish-brown spots; reduced locules in cross-section ^h	---
Aborted-pistil shape (mol.)	Apex rounded to acute ^e	Apex square to blunt, often with brown spots ^e	Apex blunt to rounded ^e
Pistillate bracteole (morph.)	Absent ^{f,h,i}	Present ^{f,h,i}	Absent or present ^{f,h,i}
Pistillate bracteole (mol.)	Absent ^e	Rounded tip, brown ^e	Colorless to pale brown tip ^e
Pistillate-hair shape and colour (morph.)	Hair-like, colorless ^{f,h}	Linear, dark tip ^{f,h}	---
Pistillate-hair shape and colour (mol.)	Linear, colorless ^e	Tip enlarged, brown ^e	Nearly linear, colorless ^e
Staminate-bracteole shape and colour (morph.)	Simple, hair-like, white ⁱ	Simple or forked, hair-like to linear, brown ⁱ	Simple or forked, hair-like, white to light brown ⁱ
Compound-pedicel shape (morph.)	Filiform, long, hair-like ^{f,h,i}	Thick, short, papillate ^{f,h,i}	Hair-like to papillate ⁱ
Compound-pedicel shape (mol.)	Filiform, long ^e	Thick, short ^e	Stout ^e
Stigma shape (morph.)	Lanceolate to ovate-lanceolate, flattened, fleshy ^{f,h,i}	Nearly linear, filiform, not fleshy ^{f,h,i}	Lance-linear, slightly fleshy ⁱ
Stigma shape (mol.)	Lanceolate to ovate-lanceolate ^e	Nearly linear ^e	Linear-lanceolate ^e

Table 1.3 Cattail leaf-lamina-margin characteristics for discrimination between *Typha latifolia*, *T. angustifolia*, and *T. x glauca*, adapted from McManus et al. (2002)

	<i>T. latifolia</i>	<i>T. angustifolia</i>	<i>T. x glauca</i>
Shape of leaf edge (oblong / wedge)	Oblong	Wedge	Wedge
Number of vascular bundles within zone of fibres at leaf edge	1	1 – 4	1 – 2
Enlargement and thickening of epidermal cells above vascular bundles	Present	Absent	Present
Arrangement of mesophyll cells (Loose arch / I-beam)	Loose arch	Loose arch to I-beam	I-beam



Fig. 1.1 Examples of cattails growing in Manitoba, 2011. **a** Emergent cattails in a prairie pothole marsh near Ninette, MB. Note the long basal leaves. **b** Cattail in flower in a prairie pothole marsh near Cartwright, MB. The male spike is above the female spike

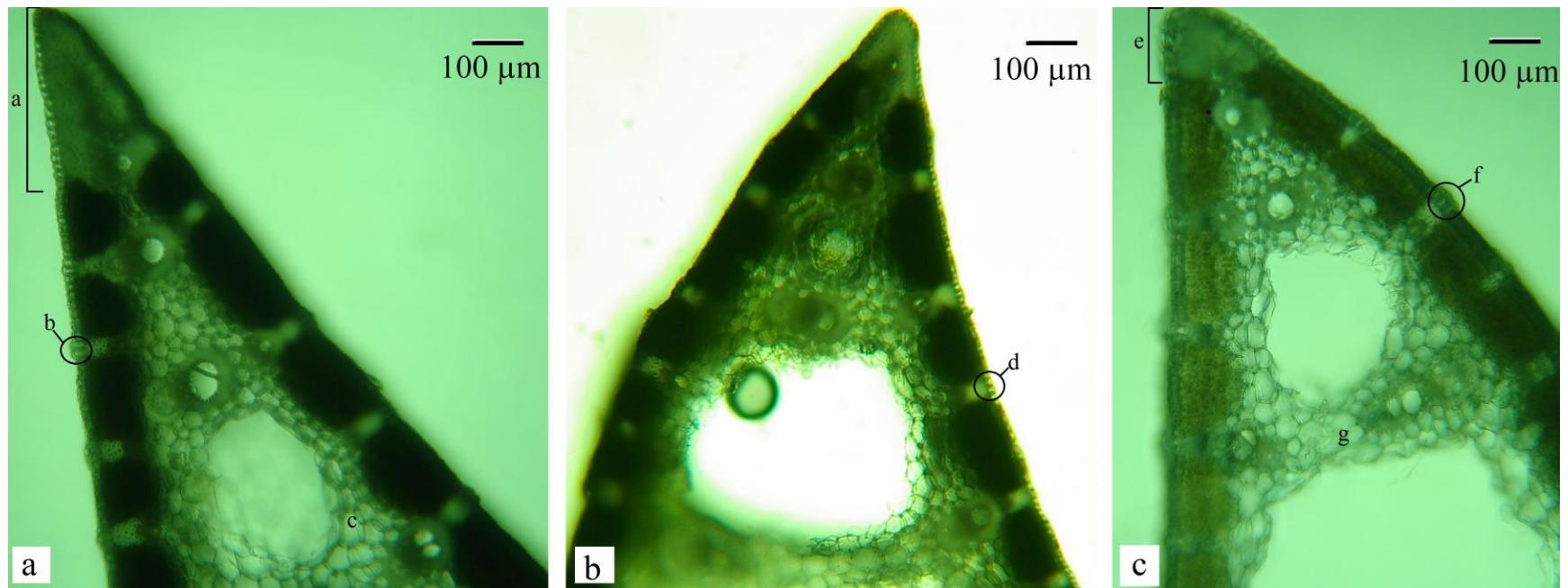


Fig. 1.2 Cattail leaf edge cross-sections viewed through a green filter. **a** *Typha latifolia*. Note the (a) oblong-shaped tip, (b) enlarged epidermal cells above the vascular bundles, and (c) more irregular arrangement of mesophyll cells. **b** *T. angustifolia*. Note the (d) absence of enlarged epidermal cells above vascular bundles. **c** *T. x glauca*. Note the (e) wedge-shaped tip, (f) enlarged epidermal cells above the vascular bundles, and the (g) I-beam arrangement of mesophyll cells

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Chapter 2. *Typha* spp. and hybrid distribution in Delta Marsh, Manitoba in 2009

Abstract

Cattails (*Typha* spp.) are invasive and tend to decrease the biodiversity and area of open water of marshes, particularly where the natural hydrological cycles have been altered, as in Delta Marsh, Manitoba. Understanding the distribution of the different cattail species and hybrids, and the environmental variables associated with their habitats, may give valuable insight into their control. In a survey of 13 transects throughout Delta Marsh, hybrid cattail, *Typha x glauca* Godr., was dominant, *T. angustifolia* L. was rare, and *T. latifolia* L. was absent. Identification was made using cytological characters of leaf cross-sections. ANOVA linear regression ($P=0.05$) revealed that above-ground biomass was correlated with mean cattail ramet height, cattail ramet density, and standing litter biomass. Cattail ramet density was negatively correlated with sampling date and positively correlated with standing litter biomass. Mean cattail height was correlated with fallen litter biomass. One-way ANOVA ($P=0.05$) revealed that fallen litter biomass was lowest in quadrats closer to the open water, and mean cattail height was greatest at the quadrats closest to the open water. While mean cattail height differed depending on whether the cattail stand was a hybrid monoculture or a mixed stand of *T. x glauca* and *T. angustifolia*, no other cattail population variables were correlated with stand type. As revealed by one-way ANOVA ($P=0.05$), water conductivity, sediment texture, total-N, nitrate-N, Olsen-P, and organic-C were not important variables in the distribution of

either *T. x glauca* or *T. angustifolia* at Delta Marsh. Therefore, managing the nutrient levels at Delta Marsh would not likely be important for limiting the distribution of *T. x glauca* in relation to *T. angustifolia*.

Introduction

Cattails (*Typha* spp.) have become of great concern to wetland managers because they displace other plant species, reducing both biodiversity and the area of open water. Both species of cattail, *T. latifolia* L. and *T. angustifolia* L. (Grace and Harrison, 1986) and their hybrid, *T. x glauca* Godr. are invasive (Galatowitsch et al., 1999). *T. latifolia* occurs throughout Canada, the range of *T. angustifolia* extends at least as far west as Central Manitoba, and the hybrid occurs wherever the range of these two species are sympatric (Grace and Harrison, 1986; Shih and Finkelstein, 2008). Understanding the distribution of the different cattail species and hybrids, and the environmental variables associated with their habitats, may give valuable insights into their control.

The mechanisms of cattail invasiveness are complex and not well understood. The main theories attribute the success of cattails to alterations of natural hydrological cycles, hybrid vigour, high production of litter, eutrophication, and land-use. Stabilized water levels have been correlated with *T. x glauca* invasion in both natural (van der Valk, 2005) wetlands and constructed/ experimental wetlands (Boers et al., 2007). However, other factors also contribute to the success that the hybrid has had in displacing native vegetation, such as stabilized water levels combined with phosphorus additions (Boers and Zedler, 2008). Cattail litter accumulation facilitates *Typha* expansion in Great Lakes wetlands with stabilized water levels (Farrer and Goldberg 2009; Vaccaro et al., 2009). In the Great Lakes region, even wetlands that have retained their historical water level fluctuations are being invaded by *T. x glauca* where there is the added pressure from

urbanization (Frieswyck and Zedler, 2007). The persistent dominance of *Typha* spp. in a lacustrine marsh in Iowa that has retained its natural water level fluctuations is attributed to both eutrophication and the invasion of common carp (*Cyprinus carpio*), which have caused higher nutrient levels, increased turbidity, and increased both sediment resuspension and disturbance (Egertson et al., 2004). Controlling the hybrid cattail is particularly challenging when the hydroperiod remains high for extended periods of time. Boers et al. (2007) found that in order for a native plant restoration to be successful, *T. x glauca* must be completely removed from a site in a constructed urban wetland in Illinois. If any hybrid cattail remained, it rapidly invaded areas seeded with native vegetation and was expected to out-compete the native flora. *T. latifolia* is resistant to herbivory by invasive juvenile common carp, which may give the native cattail a competitive advantage over other species in marshes that have also been invaded by this fish (Miller and Provenza, 2007).

Li et al. (2004) demonstrated that *T. latifolia* increased biomass production under continuous flooding conditions whereas periodic drought resulted in the reduction of both root and shoot growth. *T. x glauca* and *T. angustifolia* may be of particular concern because they can tolerate deeper water than *T. latifolia*. Both *T. x glauca* and *T. angustifolia* exhibit short rhizomes that grow densely and intertwined to form stable floating mats, enabling them to encroach into open water beyond their water depth tolerances. The rhizomes of *T. latifolia* are longer and less densely packed, so that any floating mats formed by this species tend to be short-lived, because they are easily dispersed by wind and wave action (Marsh, 1962). Wilcox and Nichols (2008) found that

a drawdown period was required for the establishment of *T. angustifolia* by seed and then a period of prolonged flooding was required for it to persist in the Great Lakes region. In areas where drought or drawdown conditions were prevalent, *T. angustifolia* decreased.

Conclusions drawn from studies where the cattails have been identified by classical morphology are confounded by possible misidentification. North American cattail species are *Typha latifolia*, *T. angustifolia*, *T. domingensis*, and *T. x glauca*. Identification of these species with morphology alone is ambiguous, especially when hybrids may be present in the population. Several studies have revealed discrepancies between morphological and molecular techniques of species identification (Lee and Fairbrothers, 1969, 1973; Lee, 1975; Suda et al., 1977; Krattinger et al., 1979; Marcinko-Kuehn and White, 1999). In contrast to gross morphology, the phenotypic expression of microscopic characters may be influenced more by genetics than the environment and therefore may be more useful for identification. Marcinko-Kuehn and White (1999) found that stigma width was more discriminating than gross morphological characters in differentiating *T. latifolia* (7-15 µm) from *T. angustifolia* (3-6 µm). The range in stigma width for *T. x glauca* (5-8 µm) overlaps with its parent species. Compound pedicel length can differentiate between *T. latifolia* (1.5-3.5 mm) and *T. angustifolia* (0.6-1.2), but differentiating either of these species from *T. x glauca* (0.5-0.7mm) is ambiguous (Hotchkiss and Dozier, 1949; Fassett and Calhoun, 1952). Marsh (1962) found that the seed characters of endosperm width, embryo length, and embryo width could be used to identify *T. latifolia* and *T. angustifolia* and the hybrid of these two species. McManus et al. (2002) found that the histochemical properties of the leaf-lamina margin differentiate

between *T. latifolia*, *T. angustifolia*, and *T. x glauca*, and that the cross-sections of the flowering stem and rhizome are unique for *T. x glauca* but not for *T. latifolia* or *T. angustifolia*. Leaf-lamina margin characters developed by McManus et al. (2002) discriminate between *T. latifolia*, *T. angustifolia*, and *T. x glauca* and because they are microscopic rather than macroscopic, their phenotypic expression is likely influenced more by genetics than by environment and should be robust across time and location. Microscopic leaf characters can be universally used to identify the species and hybrid with the advantage that it does not require the plant to be in flower.

Study site

Delta Marsh, Manitoba is an 18,500 ha freshwater coastal lacustrine marsh located along the southern edge of Lake Manitoba. This marsh provides important habitat to waterfowl and acts as a spawning and nursery area for fish species that are important to the fisheries industry (Lake Manitoba Regulation Review Advisory Committee, 2003). Delta Marsh has international recognition as it has been designated a “Wetland of International Significance” in 1982 under the Ramsar Convention, a “Manitoba Heritage Marsh” in 1988 by the Province of Manitoba, and an “Important Bird Area” in 1991 by Birdlife International (Lake Manitoba Regulation Review Advisory Committee, 2003). In addition to providing valuable habitat, Delta Marsh retains N and P from agricultural runoff that would otherwise enter Lake Manitoba (Bortoluzzi, 2013).

Water levels within Delta Marsh are directly influenced by Lake Manitoba water levels (Bortoluzzi, 2013). Since 1961, Lake Manitoba water levels have been regulated to

fluctuate by less than 0.6 m. However, before the Fairford River Water Control Structure was built at the north end of Lake Manitoba, water levels fluctuated by as much as 2 m (Lake Manitoba Regulation Review Advisory Committee, 2003). This restriction of water level oscillations is thought to have caused the replacement of *Phragmites australis* with the now-dominant *Typha* spp. (Shay et al., 1999). Since the water levels have been stabilized, waterfowl such as canvasback and lesser scaup have declined, water clarity has degraded, and algae populations, including blooming species, have increased. Common carp were first reported in Delta Marsh in the 1940s (Lake Manitoba Regulation Review Advisory Committee, 2003). *T. latifolia* have a competitive advantage over other native vegetation where carp have been introduced and water clarity has degraded (Miller and Provenza, 2007; Marsh, 1962). The muskrat population in the marsh has remained low in Delta Marsh since the 1950s, attributed to disease and the degradation of the marsh (Lake Manitoba Regulation Review Advisory Committee, 2003).

Analysis of aerial photographs revealed that the mean cover of *Typha* throughout the marsh increased from 30% in 1948 to 60% in 1980. In one pond, Crescent Pond, located in West Marsh, the estimated cover of *Typha* had increased by another 20% between 1987 and 1997. This increase in cover occurred with the displacement of *Phragmites* and the decrease in open water area (Shay et al., 1999).

The cattails at Delta Marsh were assumed to be mostly the hybrid (Shay et al., 1999). A study comparing the morphology and pollen grains of *Typha* collected throughout the West Marsh concluded that the cattail stands were composed of mostly *T. x glauca* based

on the high variability of leaf and fluorescence characteristics (Goldsborough and Zbigniewicz, 1990). However, there could also be mixed stands of the hybrid with *T. latifolia*, *T. angustifolia*, or both. Most of the pollen samples collected contained only monads, none were comprised solely of tetrads, and there was a high proportion of abortive grains. *T. latifolia* pollen consistently occurs in tetrads with low levels of abortive pollen grain, whereas both *T. angustifolia* and *T. x glauca* have high levels of abortive pollen grains and they both can have mixed pollen grains or monads (Finkelstein, 2003; Marsh, 1962). Thus, the pollen grain characteristics observed indicate that *T. latifolia* was not present in West Marsh in 1990. It is unknown when the hybrid cattail colonized the marsh. While Love and Love (1954) concluded that the only cattail species present in the early 1950s was *T. latifolia*, their observations of high variability in cattail morphology indicates that *T. x glauca*, *T. angustifolia*, or both of these species may have also been present.

Neill (1990) demonstrated that the cattails at Delta Marsh may be nitrogen-limited because they responded with increased biomass production after the addition of N or N plus P, but not to P fertilization alone. Periphyton biomass was predominately N-limited in the marsh (Bortoluzzi, 2013). Bortoluzzi (2013) found that marsh water column nutrients of total-P, Ortho-P, total-N, ammonia-N, nitrate-N, and disssolved organic-C varied throughout the marsh. She found that Lake Manitoba had a diluting effect on the nutrients within the water column, because nutrients in the marsh decreased with proximity to the lake. Nitrogen and phosphate were also being retained in the marsh

through physical and biochemical processes other than dilution. The effects of other environmental variables on the cattails at Delta Marsh are unknown.

Objectives

The objectives of this study were as follows: (1) to survey the distribution of the two *Typha* species and their hybrid throughout the marsh and to document any differences in their above-ground biomass, density, shoot height, litter biomass, or litter depth; (2) to investigate whether there were any associations between the distribution of the three cattail species and the environmental variables of sediment texture, Olsen-P, total-N, nitrate-N, organic-C, and water conductivity.

Methods

Study site

Delta Marsh, Manitoba is an 18,500 ha freshwater coastal lacustrine marsh located along the southern edge of Lake Manitoba (Fig. 2.1). The marsh is divided into three sections, West Marsh extends from the Assiniboine River Diversion to the western limit of the marsh, Centre Marsh lies between the Assiniboine River Diversion and the provincial road #240, and East Marsh extends from provincial road #240 to the eastern limit of the marsh. The East and West marshes are connected to Lake Manitoba through open water channels or culverts. Centre Marsh is connected to the East Marsh via a culvert.

Field sampling

I established 13 transects throughout Delta Marsh. Four transects were located in West Marsh, two transects in Centre Marsh, and seven in East Marsh (Fig. 2.1, Table 2.1, Appendix A). Transect locations were chosen with the requirements that they must be through cattail-dominated stands, most had to be accessible by truck or by foot, and with the goal of sampling as diverse and large of an area as possible within Delta Marsh. Both *Typha* species have different water depth tolerances (Grace and Wetzel, 1981), and so each transect was oriented along the water depth gradient, starting at the land-ward edge of the cattail stand and ending at the open water. The cattail stands at Delta Marsh grow such that there is a distinctive dense and tall band of cattails oriented along the water's edge (Waters and Shay, 1992).

At each transect, a total of six cattail ramets were collected for identification, two at each of three quadrats. Facing in the direction of the open water, the closest cattail to the center points of both the left and right edges of the quadrat were chosen for collection. Half of the specimens taken for identification were flowering, if available, and half were not flowering. For each cattail leaf collected, I recorded both the leaf width, which was measured at the widest point of the leaf, and leaf length, which was measured from where the cattail emerges from the sediment to the tip of the tallest leaf. One quadrat was placed within one meter of the water's edge, one was located at the approximate center of the dense band, and one was located within a meter of the beginning of the cattail stand at the landward edge. The three quadrats at each transect were spread out this way to increase the chances that each ramet specimen collected was from a unique genet. Unfortunately,

without genetically analyzing each specimen, there is no guarantee that all specimens collected were from unique genets. The chances of sampling multiple ramets from the same genet increases with decreasing transect length. Cattails spread quickly through clones, and an entire marsh can be comprised of one or a few genets, but mixed stands have also been observed (Grace and Harrison, 1986; Shih and Finkelstein, 2008; Olson et al., 2009). Yeo (1964) observed one seedling spread clonally to a diameter of 3 m and produce 34 mature aerial shoots within one season, and *T. x glauca* has been observed spreading clonally in the Great Lakes area at 5.2 m per year (Smith, 1967). The transect lengths varied from 6 to 270 m, but the number and relative position of the cattails collected remained constant.

One 0.25-m² quadrat was located within one meter of each pair of cattails collected for identification, for a total of three quadrats per transect. Within each quadrat, I determined above-ground biomass, cattail ramet density, percent flowering shoots, fallen litter depth, fallen litter biomass, standing litter biomass, mean shoot height, and GPS location. All shoots within the quadrat were counted, number of flowering stems recorded, and then the height of each shoot was measured from the point where it emerged from the sediment to the tip of its longest leaf. Then, all live shoots were clipped at their base and separated into flowering and not flowering stems and bagged. Standing litter that emerged from within the quadrat was clipped at its base, and all of the fallen litter within the quadrat was collected and bagged. All biomass samples were dried at 100°C until they reached a constant mass. At a point approximately one meter from the cattail stand in open water, conductivity was measured and water depth was measured.

A total of 37 quadrats across 13 transects were included in the analysis. Each transect contained three quadrats each, with the exception of transect numbers two and four, which each contained two quadrats each, with the middle quadrat omitted. The biomass within the quadrats of transects two and four was so excessive, and the locations so remote, that sampling a third quadrat at each of these transects was not possible in one trip and revisiting these locations at a later date was not possible within a reasonable time frame. Transect location was recorded as being in East, Centre, or West Marsh within Delta Marsh. Collection and field analysis took place between 7 July and 21 August 2009, when cattails should have reached maturity.

A sediment core of the top 10 cm using a soil corer was collected from the centre of each quadrat for the purpose of sediment chemical analysis. Where there was standing water present, I used my hand to cover the end of the corer to prevent the sediment from dispersing in the water as the core was retrieved. Where water was too deep to reach with my hand, a sediment core could not be retrieved. If the quadrat was located at a point where the cattails formed a floating mat, a sediment sample was not collected, and the presence of the mat was recorded. Sediment cores of sufficient volume for analysis were available from only nine sites from Delta Marsh, 2009 (Table 2.6). Sediment samples were transported on ice from the field to the laboratory.

Species and hybrid identification

From each cattail ramet collected for identification, a 5-cm section of leaf was wrapped in wet paper towel, placed in a labeled plastic bag in the field, and transported on ice to

the laboratory. Semi-permanent mounts of the leaf cross-sections in thymol-glycerin media were prepared with a hand-held razor blade on the same day of collection. The thymol-glycerin media was prepared with 75% glycerin to 25% water with a few thymol crystals added and dissolved as a preservative (Zander, 1997). The coverslip was sealed at the edges with clear nail polish to prevent desiccation. In addition, one 15-cm section of leaf from each specimen was cut into three 5-cm sections, air-dried in a leaf press, and stored in silica gel to allow for future genetic analysis. These leaf samples will be stored at University of Manitoba, Department of Biological Sciences until they have been analyzed.

The following four leaf-lamina-margin characters, adapted from McManus et al. (2002), were used to identify cattails to species are: (1) the general shape of the leaf edge, recorded as one of two categories: (i) oblong, or (ii) wedge; (2) the number of vascular bundles per leaf cross section within the zone of fibers near the leaf edge; (3) the presence or absence of thickened epidermal cells above the vascular bundles; and (4) the arrangement of the mesophyll cells connecting the adaxial and abaxial leaf surfaces, recorded as one of two categories: (i) mesophyll cells arranged in I-beam formation, or (ii) mesophyll cells arranged in a loose arch (Fig. 2.2, Table 2.2). The leaf cross-sections were viewed through a compound microscope at magnifications of 100 x and 400 x. A green filter was used to increase the contrast so that staining was not required. Pictures of all leaf cross-sections were taken with a microscope-mounted camera.

Sediment analysis

A 5-g subsample from each sediment sample was dried at 105°C to determine the moisture content to correct all sediment analyses results for moisture. All extractions were filtered with Whatman No. 42 filter papers prior to analysis.

To extract nitrate-N from the sediment, 50 mL of 2N potassium chloride and 10 g of field-moist sediment from each sample was shaken at 120 rpm for two hours and then filtered. The extract was stored frozen prior to analysis for nitrate-N concentration ($\text{mg NO}_3\text{-N kg}^{-1}$ dry sediment). Micro-segmented air flow analysis with an Astoria 2 spectrophotometer was used to perform the cadmium method for nitrate-N (Mulvaney, 1996). For each run, the cadmium reactor nitrate reduction efficiency was checked prior to analysis. Samples were analyzed only if the efficiency was between 90 and 110%. Two replicates were analyzed for each sample, and a low level standard was run every 30 samples. Replicates had an average standard deviation of $1.74 \text{ mg NO}_3\text{-N kg}^{-1}$. Calibration standards (Appendix B) were prepared with the same matrix as the samples. Results were corrected for baseline drift, blanks, carryover, and moisture content. Results were converted from $\text{mg NO}_3\text{-N L}^{-1}$ to $\text{mg NO}_3\text{-N kg}^{-1}$ dry sediment.

The remaining sediment was air dried and the samples were pooled by site and crushed to pass through a 2-mm sieve prior to further analysis. The hydrometer method was used to determine sediment texture (Carter, 1993). After passing the sediment through a 0.4-mm sieve, the loss-on-ignition method was used to determine the organic matter content which was then converted to organic-C concentration ($\text{mg organic-C kg}^{-1}$ dry sediment) (Nelson and Sommers, 1996).

To extract phosphorus from the air-dried and screened sediment, 50 mL of 0.5 M sodium bicarbonate, adjusted to pH 8.5 with sodium hydroxide, with 2.5 g of sediment was shaken at 120 rpm for two hours and then filtered. The extract was refrigerated prior to analysis for Olsen-P concentration (mg P kg^{-1} dry sediment) and total sodium bicarbonate extractable phosphorus concentration, hereafter referred to as total-P (mg P kg^{-1} dry sediment) (Kuo, 1996). The samples were adjusted to pH 6 with concentrated HCl additions prior to analysis with the Astoria 2 spectrophotometer. The extraction colour ranged from clear to dark brown. The absorbency spectrum of a subsample of light and dark coloured samples were checked with a spectrophotometer which confirmed that at least some of the samples absorbed light at 660 nm. As our methodology with the Astoria records the absorbency at 660 nm, this would result in an overestimation of Olsen-P. I ran the samples through the Olsen-P analysis procedure on the Astoria with the modification that distilled water replace the molybdenum (IV) and antimony (III) reagent. The absorbency readings of each sample without colour reagent were used as the blanks for their corresponding Olsen-P analyzed samples to correct for the absorbance of the extracts and eliminate overestimation. Two replicates were analyzed and a low level standard was run every 30 samples. Olsen-P analysis replicates had an average standard deviation of $0.17 \text{ mg P kg}^{-1}$. Concentrated HNO_3 was added to the samples to produce a 2% HNO_3 solution prior to analysis for total P using inductively coupled plasma mass spectrometry (ICP). For total P (177.434 nm), three replicates were sampled. Total-P replicates had an average standard deviation of $1.03 \text{ mg P kg}^{-1}$. Calibration standards (Appendix B) were prepared with the same matrix as the samples. Results were corrected

for moisture content and for the dilutions. Results were converted from mg P L^{-1} to mg P kg^{-1} dry sediment.

Olsen-P is a frequently used measurement for soil phosphorus, which measures the sodium bicarbonate extractable inorganic phosphorus available in the soil as orthophosphate. The ICP measures the total sodium bicarbonate extractable phosphorus available, consisting of both inorganic P, organic P, and colloidal P. Thus I would expect that the ICP-measured total-P would always be equivalent or higher than the Olsen-P inorganic phosphorus. However, six out of nine samples had lower total-P values than Olsen-P values, with the difference ranging from 2.55-46.6 mg P kg^{-1} dry sediment. A thorough methodological study is required to decipher whether total-P or Olsen-P is the more appropriate test for assessing soil phosphorus in cattail marsh sediments. This evaluation is beyond the scope of the present study. Interference of some form is assumed for detection in some of the ICP analyses, and all phosphorus measurements reported and discussed are the more widely used spectrophotometric form of Olsen-P values.

Sediment passed through a 1-mm sieve was analyzed for total C concentration (mg C kg^{-1} dry sediment) (Skjemstad and Baldock, 2008) and total N concentration (mg N kg^{-1} dry sediment) (Rutherford et al., 2008) by combustion using a Leco Tru-Spec analyzer. Samples were corrected for atmospheric moisture (0.04%). At the beginning and end of each analysis day, blanks and EDTA standards (Appendix B) were run to verify consistent and accurate results and two replicates of each sample were analyzed. The average standard deviation of replicates for total C and total N were 1.47 g C kg^{-1} and 156 mg N kg^{-1} , respectively. Six of the nine sediment samples analyzed had higher results

for organic-C than for total C, with the difference ranging from 2-176 g C kg⁻¹. Total C was removed from further analysis in favor of the more widely used organic-C values.

Statistical analysis

To reduce the effects of their skewed distributions and the effect of potential outliers, square root transformation was used for the variables total above-ground cattail biomass, non-flowering cattail biomass, standing litter biomass and litter depth. Natural logarithm transformation was used for sediment texture and nitrate-N (Fig. 2.3, 2.7). The dataset for both flowering cattail biomass and percent of shoots flowering contained many zeros, and transformation did not correct their skewed distributions. Logarithmic transformations were not suitable. Therefore, the variables of non-flowering biomass and flowering biomass were replaced with the single variable total above-ground biomass, because this eliminated the effects of the skewed distribution.

Analysis of variance (ANOVA) linear regression was used to test for correlations between the following variables: sampling date, transect length, square root of above-ground biomass, cattail density, mean cattail height, square root of standing litter biomass, fallen litter biomass, the square root of litter depth, water conductivity, the natural logarithm of sediment texture, sediment total-N, the natural logarithm of sediment nitrate-N, sediment Olsen-P, and sediment organic-C. Boxplots were used to visualize the data to ensure that their distributions were approximately normal.

One-way ANOVA was used to test for differences between the three transect locations within Delta Marsh, recorded as East Marsh, Centre Marsh, or West Marsh, with respect

to the following variables: square root of above-ground biomass, cattail density, mean cattail height, square root of standing litter biomass, and fallen litter biomass. One-way ANOVA was also used to test for differences between the three relative positions along the transects, recorded as water's edge, middle, or landward edge, with respect to the following variables: square root of above-ground biomass, cattail density, mean cattail height, square root of standing litter biomass, and fallen litter biomass. One-way ANOVA was also used to analyze whether there were differences between the transects that were *T. x glauca* monocultures and the transects that were mixtures of *T. x glauca* and *T. angustifolia* in terms of above-ground biomass, cattail density, mean cattail height, standing litter biomass, fallen litter biomass, litter depth, transect length, water conductivity, the natural logarithm of sediment texture, sediment total-N, the natural logarithm of sediment nitrate-N, sediment Olsen-P, and sediment organic-C. Levene's test was performed prior to all one-way ANOVA tests to ensure that the data met the requirement for homogeneity of variance.

All statistics were performed with the software RStudio v. 0.97.311, library car (R Core Team, 2012; Fox and Weisberg 2011). The code used for analysis with RStudio can be found in Appendix D.

Results

Ten of the 13 transects were composed of a hybrid cattail monoculture (Fig 2.1, Table 2.1). Two sites, one located in East Marsh and one in Centre Marsh, contained 83% hybrid and 17% *T. angustifolia*. One site in West Marsh contained 33% *T. x glauca* and

67% *T. angustifolia*. *T. latifolia* was not identified in any transect at Delta Marsh. Three transects terminated in a cattail floating mat where the cattails met the open water. Water depth in the open water, 1 m from the cattail stand ranged from 0 – 78 cm (Table 2.1).

Cattail density, shoot height, above-ground biomass, standing litter biomass, fallen litter biomass, fallen litter depth, and percent of flowering shoots all exhibited large ranges with large standard deviations relative to their means both within transects and among transects (Tables 2.1 and 2.3). ANOVA linear regression F-tests revealed that sampling date was negatively correlated with cattail density ($P=0.036$, $r^2=0.120$) (Fig. 2.4A).

Square root of above-ground biomass was positively correlated with the following variables: square root of standing litter biomass ($P=0.018$, $r^2=0.151$), mean cattail height ($P=2.51 \times e^{-05}$, $r^2=0.402$), and cattail density ($3.22 \times e^{-04}$, $r^2=0.313$) (Fig. 2.4B, C, D).

Density was correlated with square root of standing litter biomass ($P=0.027$, $r^2=0.131$) (Fig. 2.5A). Mean cattail height was negatively correlated with fallen litter biomass ($P=0.031$, $r^2=0.126$) (Fig. 2.5B), and fallen litter biomass was positively correlated with square root of litter depth ($P=1.06 \times e^{-07}$, $r^2=0.559$) (Fig. 2.5C). There were no other correlations between the above-listed variables at the $P=0.05$ significance level (Table 2.4).

One-way ANOVA F-tests revealed that the three locations in the marsh did not differ in their above-ground biomass, standing litter biomass, fallen litter biomass, or fallen litter depth. Levene's test for homogeneity of variance revealed that both density and height did not display homogeneity of variance when grouped by location in the marsh (East,

Centre, or West). Therefore one-way ANOVA could not be used to analyze the relationships between location and either cattail density or height (Table 2.5).

Both mean cattail height and fallen litter biomass was correlated with the relative position along the transects ($P=0.020$, $P=0.014$) (Table 2.5, Fig 2.6). One-way ANOVA could not be used to analyze the relationship between square root of litter depth and the relative position along the transects (land, middle, or water) because the variance across the groups for was not homogeneous according to the results of the Levene's test (Table 2.5).

Mean cattail height was taller in stand types of *T. x glauca* monoculture than mixed stands of *T. x glauca* and *T. angustifolia* ($P=0.031$) (Table 2.5, Fig. 2.6C).

Throughout Delta Marsh, the following environmental variables had large ranges: transect length, water conductivity, and sediment texture, organic-C, total-N, nitrate-N, and Olsen-P (Table 2.6). ANOVA linear regression of all combinations of the above-listed environmental variables and the cattail variables revealed that sediment total-N was correlated with the natural logarithm of sediment texture ($P=0.021$, $r^2=0.556$). Sediment Olsen-P was positively correlated with both the natural logarithm of nitrate-N ($P=0.046$, $r^2=0.457$) and negatively correlated with square root of standing litter biomass ($P=0.003$, $r^2=0.728$) (Tables 2.7 and 2.8, Fig. 2.8). The natural logarithm of sediment nitrate-N was also correlated with square root of standing litter biomass ($P=0.020$, $r^2=0.562$) (Table 2.8, Fig. 2.8). None of these environmental variables differed by stand type at the $P=0.05$ significance level (Table 2.9).

Discussion

In 2009, the cattail stands of Delta Marsh were dominated by *T. x glauca* as expected from previous studies (Goldsborough and Zbigniewicz, 1990; Shay et al, 1999) but *T. angustifolia* was also present. The dynamics of the *T. angustifolia* and *T. x glauca* mixed stands are unknown, because this study took place over only one season. Further research is needed to assess whether *T. angustifolia* will be able to compete with the hybrid, or whether it will eventually disappear from the marsh. *T. latifolia* is capable of out-competing *T. angustifolia* at lower water levels in an oligotrophic pond (Grace and Wetzel, 1998), but, in an eutrophic lake, *T. angustifolia* displaced *T. latifolia* in all but the most shallow water depths (Weisner, 1993). No published studies have investigated competition between *T. x glauca* and its parent species. In this study, there were no differences in nutrient levels between mixed *Typha* species stands and hybrid monocultures. Assuming that nutrients drive competition, I cannot predict the outcome of competition between the hybrid and *T. angustifolia*.

Because above-ground biomass, standing litter biomass, fallen litter biomass, and fallen litter depth did not vary between East, Centre and West marshes, conclusions about these variables made at one location in Delta Marsh are representative throughout this marsh.

While sampling date was negatively correlated with cattail density ($p=0.036$), the correlation was weak ($r^2=0.120$). Cattail density declined with sampling date, but the spread of data points around the regression line was large, and the regression only accounted for 12% of the variation of cattail density. Thus, while this correlation is statistically significant, its biological significance is questionable.

Mean cattail biomass of 972 g m⁻² found here was within the range of 747-1790 g m⁻², reported for the cattail stands at Delta Marsh in 1985-1986 (Waters and Shay, 1990). The same study reported mean cattail shoot density in Crescent Pond, Delta Marsh, as ranging from 12-41 shoots m⁻², which is lower than the mean of 57 cattail shoots m⁻² found in this study. The six quadrats in Crescent Pond from the present study had cattail densities ranging from 44 to 64 cattail shoots m⁻². Cattail shoot heights ranged from 124-207 cm in this current study and cattail height ranged from 127 – 336 cm in 1985-1986 (Waters and Shay, 1990). Differences in study design between the current study and that by Waters and Shay (1990), do not allow for direct comparisons. Waters and Shay (1990) sampled in long term plots that did not necessarily go to the water's edge, or go through the band of dense cattails along the water's edge. Because my transect sampling design purposely sampled within this dense band, my cattail densities and heights may be inflated compared to those of Waters and Shay (1990).

Mean shoot height was negatively correlated with fallen litter biomass. Height also varies with water depth (Waters and Shay, 1990), although this was not tested in my study. Water depths between sites could not be directly compared because they would vary throughout the season. Sampling occurred over two months, and each location in the marsh was only visited once. Water depth would have varied with seasonal drying and with heavy rain events as well as with basin morphometry.

The positive correlations between above-ground biomass and both shoot height ($P=2.51 \times e^{-05}$, $r^2=0.402$) and shoot density ($P=3.22 \times e^{-04}$, $r^2=0.313$) were weak, both accounting for less than 50% of the variation in above-ground biomass. Therefore, neither shoot height

nor shoot density were good indicators of above-ground biomass. The increase in cattail ramet height at the water's edge was observed in this study, as well as in 1985 -1986 (Waters and Shay, 1992). The authors hypothesized that an edge effect, with increased light and nutrient availability, and juvenile ramets was likely responsible for the band of taller cattails along the water's edge.

The positive correlation between above-ground biomass and standing litter biomass was weak ($P=0.018$, $r^2=0.151$), with most points lying outside of the 95% confidence interval. However, there was a strong positive correlation between cattail density and the square root of standing litter biomass ($(P=1.06 \times e^{-07}, r^2=0.559)$, with approximately 60% of the variation in cattail density being accounted for by the square root of standing litter biomass. Three transects terminated with a floating mat at the water's edge, and so the biomass production at those quadrats would not have been limited by the amount of aerating standing litter present. Standing litter provides oxygen to the tissues that are under water and subject to anaerobic conditions. Removal of the standing litter decreases biomass production when the rhizomes are under water but not when the rhizomes have access to oxygen, which will occur if there is no water or if the rhizomes are near the water surface within a floating mat (Marsh, 1962). An edge effect near the open water, where litter may be removed by wave action, could reduce the correlation between biomass and standing litter.

The lack of correlation between above-ground cattail biomass and either fallen litter depth or fallen litter biomass indicates that cattail production in Delta Marsh was not affected by the deposition of its own litter. However, there was a weak negative

correlation between fallen litter biomass and mean cattail height ($P=0.031$, $r^2=0.126$).

Thus, while litter did not adversely affect biomass production, it reduced the average cattail ramet height. Fallen litter depth was lowest in quadrats close to the water's edge along the transects. At the open water edge, wind may disperse the fallen litter. Jordan et al. (1990) found that when litter depths exceeded 50 cm, the biomass of *T. angustifolia* was reduced. The litter layer at Delta Marsh was well below 50 cm, so it would not be expected to reduce cattail biomass. A previous study (Waters and Shay, 1992) also concluded that the cattails at Delta Marsh were not self-thinning. With the litter depth averaging 7 cm deep and approximately 700 g m^{-2} , the cattail litter layer may help to exclude other species and assist its invasion into new territory as has been observed at other lacustrine marshes (Farrer and Goldberg, 2009; Vaccaro et al., 2009).

The strong positive correlation between the square root of litter depth and fallen litter biomass ($P=1.06 \times e^{-07}$, $r^2=0.559$) was expected, because they are both measurements of fallen litter. Increasing the number of replicates of fallen litter depth measurements should strengthen the correlation further.

Mean cattail height was the only cattail variable that differed between the monoculture *T. x glauca* and mixed *T. x glauca* and *T. angustifolia* stand types. As expected, mixed stands had a lower average height than hybrid monocultures. *T. angustifolia* is shorter than the hybrid (Smith, 1967).

The large ranges of the water and sediment variables indicate that *T. x glauca* and *T. angustifolia* grow under varying environmental conditions. In this study, conductivity varied from $533 - 1120 \mu\text{S cm}^{-1}$, which is lower than the $743 - 2801 \mu\text{S cm}^{-1}$ range found

by Bortoluzzi (2013) from 2003 to 2005. Bortoluzzi (2013) found that conductivity varied with year, decreasing in higher water years. The year of my study, 2009, was a high water year, and conductivity levels were expected to be lower due to dilution effects. Soil solution is saline when the conductivity is greater than 2000 to 4000 $\mu\text{S cm}^{-1}$, with only salt-sensitive crops demonstrating adverse effects under 4000 $\mu\text{S cm}^{-1}$ (Manitoba Agriculture, Food and Rural Development, 2014). Because the sites at my study were non-saline, conductivity was not expected to adversely affect the cattails.

While Olsen-P accounted for only approximately 46% of the natural logarithm of nitrate-N ($P=0.046$, $r^2=0.457$), the majority of the data points lie within the 95% confidence interval, so this correlation was strong. The negative correlations were strong between the square root of standing litter biomass and both Olsen-P ($P=0.003$, $r^2=0.728$) and the natural logarithm of nitrate-N ($P=0.020$, $r^2=0.562$). However, no other cattail population variables were correlated with the environmental variables. The negative correlation between standing litter biomass and the two nutrient variables of Olsen-P and Ln of nitrate-N was likely due to there being less litter near the water and perhaps more nutrients near the water. Because the sediment was pooled for each transect, I cannot verify whether the nutrients were more abundant near the water than at other positions along the transects.

The sediments ranged from 4 – 24% organic-C (Table 2.6). Soil is classified as organic when the organic-C content is greater than 17% (Soil Classification Working Group, 1998), and therefore much of the sediment at Delta Marsh was high in organic-C. Corresponding to the high organic-C content, total-N was also high, ranging from 3.3 to

16.7 g-N kg⁻¹ sediment. The marsh sediments were fertile, with nitrate-N ranging from 1.6 to 85.1 mg-NO₃ -N kg⁻¹ sediment, and Olsen-P ranging from 4.2 to 38.2 mg-Olsen-P kg⁻¹ sediment, assuming that the changes in redox condition did not severely affect the results. For comparison, Government of Manitoba (2007) recommends that fertilizer be applied to soils for growing corn when NO₃ -N is under 25 mg-NO₃ -N kg⁻¹ soil and Olsen-P is considered to be at low levels when under 10 mg-Olsen-P kg⁻¹ soil. Because the sediments were fertile, cattails in general were expected to thrive.

There were no differences in any of the environmental parameters when grouped according to stand type. Therefore, the presence or absence of *T. x glauca* versus *T. angustifolia* was not correlated with water conductivity, sediment total-N, nitrate-N, Olsen-P or organic-C at Delta Marsh. Whether this can be extrapolated to all Manitoba freshwater lacustrine marshes, or to pothole marshes, needs to be investigated.

Correlations between these variables and *T. latifolia* also need to be studied. *T. x glauca* may be capable of luxuriant uptake of nutrients (Waters and Shay, 1990), enabling it to flourish where the availability of the nutrients fluctuates. In Virginia, Bevington (2007) found no differences between created wetlands with cattails present and with cattails absent in terms of soil organic matter, total-P, or total-N. Svengsouk and Mitsch (2001) found that *T. latifolia* outcompeted *Schoenoplectus tabernaemontani* under eutrophic conditions but not under oligotrophic conditions. Eutrophication has been demonstrated to benefit *T. x glauca* and be detrimental to other wetland macrophytes in fertilization studies (Woo and Zedler, 2002). In Great Lakes coastal marshes, the success of *T. x glauca* has been attributed to increased nutrient availability due to hydrological

disturbances (Zedler and Kercher, 2004). Thus, the importance of nutrients for cattail distribution varies for different marsh systems.

Phosphorus and nitrogen bioavailability in wetland sediment vary as the redox potential varies with changes in sediment moisture throughout the season. These changes are particularly pronounced when sediment goes from anaerobic to aerobic or vice versa (Mitsch and Gosselink, 2000). Sampling methods such as the in situ resin method used by Nelson et al. (2007) more accurately reflect the bioavailability of nutrients such as P and N over time than the methods used in this study. In particular, during the process of air-drying, anaerobic sediment becomes aerobic and the forms of P and N can change as a result of the redox potential change. While the resin-P method is more accurate, it was not known to me at the time and so I performed the older methods that were routinely used. The benefit of these older methods is that they allow for direct comparisons with other studies that used the same methods.

The leaf-lamina-margin identification method was chosen, because it was more accurate than using gross external morphology, and because genetic analysis was unavailable. The method has the advantage that it relies on characters within vegetative tissue, which expands the available sampling window to when leaves are mature to their senescence, rather than limiting it to when the plants are in flower. The method also allowed for less biased sampling because even marshes that did not have cattails in flower could be sampled, rather than being limited to those specimens in flower. While it does have a number of advantages, the leaf-lamina-margin method has only been used by one previous study, in one location (McManus et al., 2002). In that study, however, the leaf-

lamina-margin method was validated by genetic analysis. The frequency distributions of leaf width (Fig. 2.9) and logarithm of leaf length/leaf width (Fig. 2.10) of 416 cattail ramets collected in southwestern Manitoba and southeastern Saskatchewan in 2009 and 2011 as identified with leaf-lamina-margin method also support this method. Out of the 416 cattail ramets, 331 specimens were *T. x glauca*, 80 were *T. latifolia*, and 5 were *T. angustifolia*. The frequency distributions for both leaf widths and logarithm leaf length/leaf width of *T. latifolia* and *T. angustifolia* overlap, but their peaks are separate. The frequency distributions of leaf width for *T. x glauca* overlaps both *T. latifolia* and *T. angustifolia*, as expected. The frequency distributions of logarithm leaf length/leaf width for *T. x glauca* overlaps both *T. latifolia* and *T. angustifolia*. The frequency distribution of *T. angustifolia* logarithm leaf length/leaf width has two peaks, where one peak coincides with the peak for *T. x glauca*. This unexpected peak for *T. angustifolia* is the result of just one sample at Delta Marsh in 2009. This specimen may be either a misidentified *T. x glauca* specimen, or it may be a correctly identified *T. angustifolia* specimen with a logarithm leaf length/leaf width comparable to *T. x glauca*. Genetic analysis is required to resolve this issue. The leaf-lamina-margin method has great potential for accurate cattail identification where genetic analysis is not available, but it does need further validation through genetic analysis of cattails in different regions.

This study demonstrates the plasticity of cattails. The cattails of Delta Marsh are dominant in areas that are both high and low in all of the environmental variables examined in this study. Cattails appear to respond to variations in standing and fallen litter by altering their height and density, although this could also be in response to water

depth. Because this study took place over only one season, cause and effect relationships cannot be assessed. Longer term experimental studies are required to determine causes and effects. An experimental macrocosm study that investigates the differences between *T. x glauca*, *T. latifolia*, and *T. angustifolia* and their responses to competition and the range of environmental variables that they are exposed to at Delta Marsh would be useful to study these complex interactions, because naturally occurring *T. angustifolia* is rare and *T. latifolia* is non-existent at this marsh.

The mechanisms behind the cattail invasion at Delta Marsh require further study. The stabilized water levels of Lake Manitoba, the large amounts of litter produced by cattails, and their resistance to carp herbivory are likely important factors in the cattails' success. Sediment texture, nutrient levels, and water conductivity are not important factors for the cattail distributions in this system, at least when comparing the distribution of *T. x glauca* to *T. angustifolia*. However, these factors could be important to other cattail systems, or for the distribution of *T. latifolia* elsewhere, because these were not investigated in this study. Given that *T. latifolia*, *T. angustifolia*, (Grace and Wetzel, 1981) and *T. x glauca* (Waters and Shay, 1992) have different water depth tolerances, basin morphometry is also likely important. Further research into these mechanisms will benefit managers as they form plans to restore native vegetation in marshes.

Table 2.1 Transect number, location (West, Centre, East) and length; sampling date; percentages of *Typha x glauca* and *T. angustifolia*; maximum water depth; whether transects terminated in a floating mat; and the mean and standard deviations for the following parameters: cattail density, percent of flowering shoots, shoot height, above-ground biomass, standing litter biomass, fallen litter biomass, and fallen litter depth for 13 transects in 2009 at Delta Marsh, MB. Transects number two and four contained two quadrats and all other transects contained three quadrats, oriented along the water depth gradient. For a map of transect locations, see Fig. 2.1. For the GPS coordinates, see Appendix A

Transect #	Date	Location	<i>T. x glauca</i> (%)	<i>T. angustifolia</i> (%)	Transect length (m)	Water depth (cm)	Floating mat present	Density (shoots m ⁻²)	Shoot height (cm)	Total above- ground biomass (g m ⁻²)	Standing litter biomass (g m ⁻²)	Fallen litter biomass (g m ⁻²)	Fallen litter depth (cm)
								Mean ± Std. Dev.	Mean ± Std. Dev.	Mean ± Std. Dev.	Mean ± Std. Dev.	Mean ± Std. Dev.	Mean ± Std. Dev.
1	7-Jul	W	100	0	270	61	yes	63 ± 2.3	149.4 ± 41.3	677.6 ± 426.0	611.5 ± 156.9	877.1 ± 769.7	6 ± 4.9
2	10-Jul	C	100	0	11	40	yes	56 ± 5.7	176.4 ± 16.8	461.6 ± 44.1	834.2 ± 595.4	670.2 ± 947.8	6 ± 7.8
3	15-Jul	E	100	0	15	57	no	33 ± 31.1	137.6 ± 44.5	360.8 ± 261.7	19.7 ± 34.2	462.9 ± 723.3	3 ± 4.2
4	16-Jul	E	100	0	9	16	no	86 ± 31.1	206.8 ± 45.0	1918.8 ± 1066.3	829.4 ± 777.0	550.2 ± 778.1	6 ± 8.5
5	17-Jul	E	100	0	6	40	no	97 ± 19.7	183.3 ± 66.5	1061.5 ± 241.9	632.9 ± 326.5	990.3 ± 398.0	12 ± 5.5
6	21-Jul	W	100	0	70	2	no	65 ± 27.2	108.3 ± 39.6	631.6 ± 371.4	350.8 ± 375.2	906.4 ± 161.1	10 ± 5.0
7	24-Jul	E	100	0	56	43	no	53 ± 2.3	171.7 ± 48.6	610.1 ± 288.6	374.0 ± 139.4	1194.4 ± 749.2	14 ± 1.2
8	27-Jul	C	83	17	214	13	no	49 ± 6.1	187.5 ± 32.1	701.1 ± 282.5	356.3 ± 234.5	719.2 ± 165.3	8 ± 1.0
9	29-Jul	E	100	0	130	78	yes	39 ± 23.1	149.5 ± 13.9	786.1 ± 765.0	666.3 ± 611.5	269.9 ± 147.5	3 ± 1.7
10	31-Jul	E	83	17	12	0	no	31 ± 12.2	205.5 ± 14.3	733.2 ± 96.3	0.0 ± 0.0	471.7 ± 271.1	6 ± 6.2
11	4-Aug	W	100	0	70	27	no	53 ± 8.3	167.0 ± 85.0	740.3 ± 505.9	76.9 ± 133.3	998.1 ± 214.1	15 ± 13.0
12	6-Aug	E	100	0	52	3	no	33 ± 10.1	124.4 ± 33.1	697.3 ± 345.4	461.3 ± 360.1	862.5 ± 350.0	6 ± 2.1
13	7-Aug	W	33	67	10	20	no	56 ± 21.2	256.9 ± 10.6	1079.2 ± 125.1	807.2 ± 463.4	646.0 ± 221.9	6 ± 1.0

Table 2.2 Cattail leaf-lamina-margin characters for discrimination between *Typha latifolia*, *T. angustifolia*, and *T. x glauca*, adapted from McManus et al. (2002)

	<i>T. latifolia</i>	<i>T. angustifolia</i>	<i>T. x glauca</i>
Shape of leaf edge (oblong / wedge)	Oblong	Wedgevv	Wedge
Number of vascular bundles within zone of fibres at leaf edge	1	1 – 4	1 – 2
Enlargement and thickening of epidermal cells above vascular bundles	Present	Absent	Present
Arrangement of mesophyll cells (Loose arch / I-beam)	Loose arch	Loose arch to I-beam	I-beam

Table 2.3 Minimum, maximum, mean, and standard deviation of cattail shoot density, percent flowering shoots, shoot height, total above-ground biomass, standing litter biomass, fallen litter biomass, and fallen litter depth from 37 quadrats within 13 transects from Delta Marsh, Manitoba, 2009 (n=37). For a map of transect locations, see Fig. 2.1. For the GPS coordinates of all quadrats, see Appendix A.

	Density (shoots m ⁻²)	Flowering shoots (%)	Shoot height (cm)	Above-ground biomass (g m ⁻²)	Standing litter biomass (g m ⁻²)	Fallen litter biomass (g m ⁻²)	Fallen litter depth (cm)
Min	8	0.0	65.0	88.4	0.0	0.0	0
Max	120	77.0	269.0	2672.8	1378.8	1669.6	30
Mean	54	8.0	170.0	783.7	443.2	746.9	8
Std. Dev.	24	15.2	52.7	482.8	410.4	480.6	6

Table 2.4 ANOVA linear regression of all combinations of the following cattail variables: mean height, density, square root of above-ground biomass, square root of standing litter biomass, fallen litter biomass and square root of litter depth, n=37. Regression and residual degrees of freedom for all analyses are 1 and 35, respectively

X variable	Y variable	F	P	r ²
Date	SQRT above-ground biomass	0.353	0.557	0.010
Date	SQRT standing litter biomass	1.159	0.289	0.032
Date	Fallen litter biomass	0.017	0.898	0.000
Date	SQRT litter depth	1.636	0.209	0.045
Date	Cattail density	4.765	0.036	0.120
Date	Cattail height	1.467	0.234	0.040
SQRT standing litter biomass	SQRT above-ground biomass	6.203	0.018	0.151
Fallen litter biomass	SQRT above-ground biomass	2.054	0.161	0.055
SQRT litter depth	SQRT above-ground biomass	2.012	0.165	0.054
Height	SQRT above-ground biomass	23.541	2.51E-05	0.402
Density	SQRT above-ground biomass	15.917	3.22E-04	0.313
SQRT standing litter biomass	Density	5.293	0.027	0.131
Fallen litter biomass	Density	0.559	0.460	0.016
SQRT litter depth	Density	0.068	0.796	0.002
Height	Density	0.699	0.409	0.020
Fallen litter biomass	Height	5.049	0.031	0.126
SQRT litter depth	Fallen litter biomass	44.320	1.06E-07	0.559
SQRT standing litter biomass	Fallen litter biomass	0.048	0.827	0.001
SQRT standing litter biomass	Height	2.308	0.138	0.062
SQRT standing litter biomass	SQRT litter depth	1.716	0.199	0.047
SQRT litter depth	Height	2.138	0.153	0.058

Table 2.5 Levene's test for homogeneity of variance and one-way ANOVA for each of location in the marsh, position along the transects, and stand type, with the following cattail variables: mean height, density, square root above-ground biomass, square root standing litter biomass, fallen litter biomass, and square root litter depth, n=37

X variable	Y variable	Regression, residual d.f.	Levene's Test		ANOVA	
			F	P	F	P
Location	SQRT above-ground biomass	2, 34	0.736	0.487	0.250	0.776
Location	SQRT standing litter biomass	2, 34	1.457	0.247	0.622	0.543
Location	Fallen litter biomass	2, 34	1.810	0.179	0.451	0.641
Location	Density	2, 34	3.571	0.039	NA	NA
Location	Height	2, 34	5.739	0.007	NA	NA
Location	SQRT litter depth	2, 34	0.354	0.705	0.374	0.691
Position	SQRT above-ground biomass	2, 34	1.667	0.204	2.243	0.122
Position	SQRT standing litter biomass	2, 34	0.378	0.688	0.121	0.886
Position	Fallen litter biomass	2, 34	0.086	0.918	4.830	0.014
Position	Density	2, 34	0.625	0.542	0.088	0.916
Position	Height	2, 34	0.811	0.453	4.407	0.020
Position	SQRT litter depth	2, 34	3.460	0.043	NA	NA
Stand type	SQRT above-ground biomass	1, 35	2.478	0.125	0.684	0.414
Stand type	SQRT standing litter biomass	1, 35	0.138	0.713	0.007	0.936
Stand type	Fallen litter biomass	1, 35	1.553	0.221	0.421	0.521
Stand type	Density	1, 35	0.528	0.472	0.060	0.808
Stand type	Height	1, 35	0.025	0.874	5.026	0.031

Table 2.6 Summary of environmental variables at nine Delta Marsh transects, 2009, of transect length, stand type, water conductivity, sediment texture, sediment organic-C, sediment total-N, sediment nitrate-N, sediment Olsen-P. The average standard deviation of replicate samples is shown in brackets in the column headings where applicable.

Date	Transect #	Transect length (m)	Stand type	Water Conductivity ($\mu\text{S cm}^{-1}$)	Texture (% Clay)	Organic C (g-organic-C kg $^{-1}$)	Total-N (g-N kg $^{-1}$) (± 0.16)	Nitrate-N (mg-NO $_{3-N}$ kg $^{-1}$) (± 1.7)	Olsen-P (mg-Olsen-P kg $^{-1}$) (± 0.2)
Jul 08	1	270	Monoculture	955	3	184.4	16.2	8.9	26.2
Jul 17	5	6	Monoculture	1071	3	117.1	14.2	1.6	6.0
Jul 21	6	70	Monoculture	533	17	77.9	6.6	16.3	19.2
Jul 27	8	214	Mixed	1001	7	243.8	6.4	28.0	18.1
Jul 29	9	130	Monoculture	1022	3	98.0	8.7	14.3	11.8
	1								
Jul 31	0	12	Mixed	NA	7	154.7	12.9	85.1	38.4
	1								
Aug 04	1	70	Monoculture	900	6	195.3	16.1	54.3	35.8
	1								
Aug 06	2	52	Monoculture	1120	3	200.7	16.7	19.2	7.4
	1								
Aug 07	3	10	Mixed	1001	23	41.1	3.3	14.3	4.2
Minimum		6		533	3	41.1	3.3	1.6	4.2
Maximum		270		1120	23	243.8	16.7	85.1	38.4

Table 2.7 ANOVA linear regression of all combinations of the following variables: sampling date, transect length, water conductivity, Ln of sediment texture, total-N, Ln of nitrate-N, organic-C, and Olsen-P, n=9. The r^2 shown for significant results ($P = 0.05$)

X variable	Y variable		Regression, residual		
		d.f.	F	P	r^2
Transect length	Date	1, 7	2.951	0.130	---
Water conductivity	Date	1, 6	0.362	0.570	---
Ln of sediment texture	Date	1, 7	0.891	0.377	---
Sediment total-N	Date	1, 7	0.347	0.574	---
Ln of sediment nitrate-N	Date	1, 7	3.409	0.107	---
Sediment Olsen-P	Date	1, 7	0.055	0.822	---
Sediment organic-C	Date	1, 7	0.023	0.883	---
Water conductivity	Transect Length	1, 6	0.001	0.980	---
Sediment texture	Transect Length	1, 7	0.807	0.399	---
Sediment total-N	Transect Length	1, 7	0.025	0.879	---
Ln of sediment nitrate-N	Transect Length	1, 7	0.000	0.985	---
Sediment Olsen-P	Transect Length	1, 7	0.249	0.633	---
Sediment texture	Water conductivity	1, 6	2.462	0.161	---
Sediment total-N	Water conductivity	1, 6	0.673	0.443	---
Ln of sediment nitrate-N	Water conductivity	1, 6	0.328	0.588	---
Sediment Olsen-P	Water conductivity	1, 6	1.230	0.310	---
Sediment organic-C	Water conductivity	1, 6	0.648	0.452	---
Sediment total-N	Sediment texture	1, 7	8.770	0.021	0.556
Ln of sediment nitrate-N	Sediment texture	1, 7	0.729	0.421	---
Sediment Olsen-P	Sediment texture	1, 7	0.000	0.996	---
Sediment organic-C	Sediment texture	1, 7	3.219	0.172	---
Ln of sediment nitrate-N	Sediment total-N	1, 7	0.008	0.930	---
Sediment Olsen-P	Sediment total-N	1, 7	1.079	0.334	---
Sediment organic-C	Sediment total-N	1, 7	2.890	0.133	---
Sediment Olsen-P	Ln of sediment nitrate-N	1, 7	5.892	0.046	0.457
Sediment organic-C	Ln of sediment nitrate-N	1, 7	0.818	0.396	---
Sediment organic-C	Sediment Olsen-P	1, 7	1.479	0.263	---

Table 2.8 ANOVA linear regression of transect length, water conductivity, Ln of sediment texture, total-N, Ln of nitrate-N, organic-C, and Olsen-P, each with the following variables: square root of above-ground biomass, fallen litter biomass, square root of standing litter biomass, and mean cattail shoot height, n=9. The r^2 shown for significant results ($P = 0.05$), regression and residual degrees of freedom (1, 7)

X variable	Y variable	F	P	r^2
Transect length	SQRT above-ground biomass	0.002	0.963	---
Water conductivity	SQRT above-ground biomass	1.717	0.238	---
Ln of sediment texture	SQRT above-ground biomass	0.399	0.548	---
Sediment total-N	SQRT above-ground biomass	0.387	0.553	---
Ln of sediment nitrate-N	SQRT above-ground biomass	1.789	0.223	---
Sediment Olsen-P	SQRT above-ground biomass	1.481	0.263	---
Sediment organic-C	SQRT above-ground biomass	2.177	0.184	---
Transect length	Fallen litter biomass	0.001	0.972	---
Water conductivity	Fallen litter biomass	0.335	0.584	---
Ln of sediment texture	Fallen litter biomass	0.002	0.964	---
Sediment total-N	Fallen litter biomass	1.467	0.265	---
Ln of sediment nitrate-N	Fallen litter biomass	0.807	0.399	---
Sediment Olsen-P	Fallen litter biomass	0.001	0.976	---
Sediment organic-C	Fallen litter biomass	0.504	0.501	---
Transect length	SQRT standing litter biomass	0.400	0.547	---
Water conductivity	SQRT standing litter biomass	0.860	0.390	---
Ln of sediment texture	SQRT standing litter biomass	0.059	0.815	---
Sediment total-N	SQRT standing litter biomass	0.694	0.432	---
Ln of sediment nitrate-N	SQRT standing litter biomass	8.967	0.020	0.562
Sediment Olsen-P	SQRT standing litter biomass	18.742	0.003	0.728
Sediment organic-C	SQRT standing litter biomass	1.097	0.330	---
Transect length	Height	0.699	0.430	---
Water conductivity	Height	1.175	0.320	---
Ln of sediment texture	Height	1.351	0.283	---
Sediment total-N	Height	1.250	0.301	---
Ln of sediment nitrate-N	Height	0.034	0.858	---
Sediment Olsen-P	Height	0.035	0.857	---
Sediment organic-C	Height	0.430	0.533	---

Table 2.9 Levene's test for homogeneity of variance and one-way ANOVA for the following variables grouped according to stand type: transect length, water conductivity, natural logarithm of sediment texture, total-N, natural logarithm of nitrate-N, organic-C, and Olsen-P, n=9; regression, residual degrees of freedom (1, 7)

X variable	Y variable	Levene's Test		ANOVA	
		F	P	F	P
Stand type	Transect length	0.402	0.546	0.088	0.775
Stand type	Water conductivity	1.923	0.215	0.183	0.683
Stand type	Ln of sediment texture	0.001	0.972	2.897	0.133
Stand type	Sediment total-N	0.001	0.983	3.025	0.126
Stand type	Ln of sediment nitrate-N	0.118	0.742	1.487	0.262
Stand type	Sediment Olsen-P	0.350	0.573	0.069	0.801
Stand type	Sediment organic-C	1.044	0.341	0.000	0.985

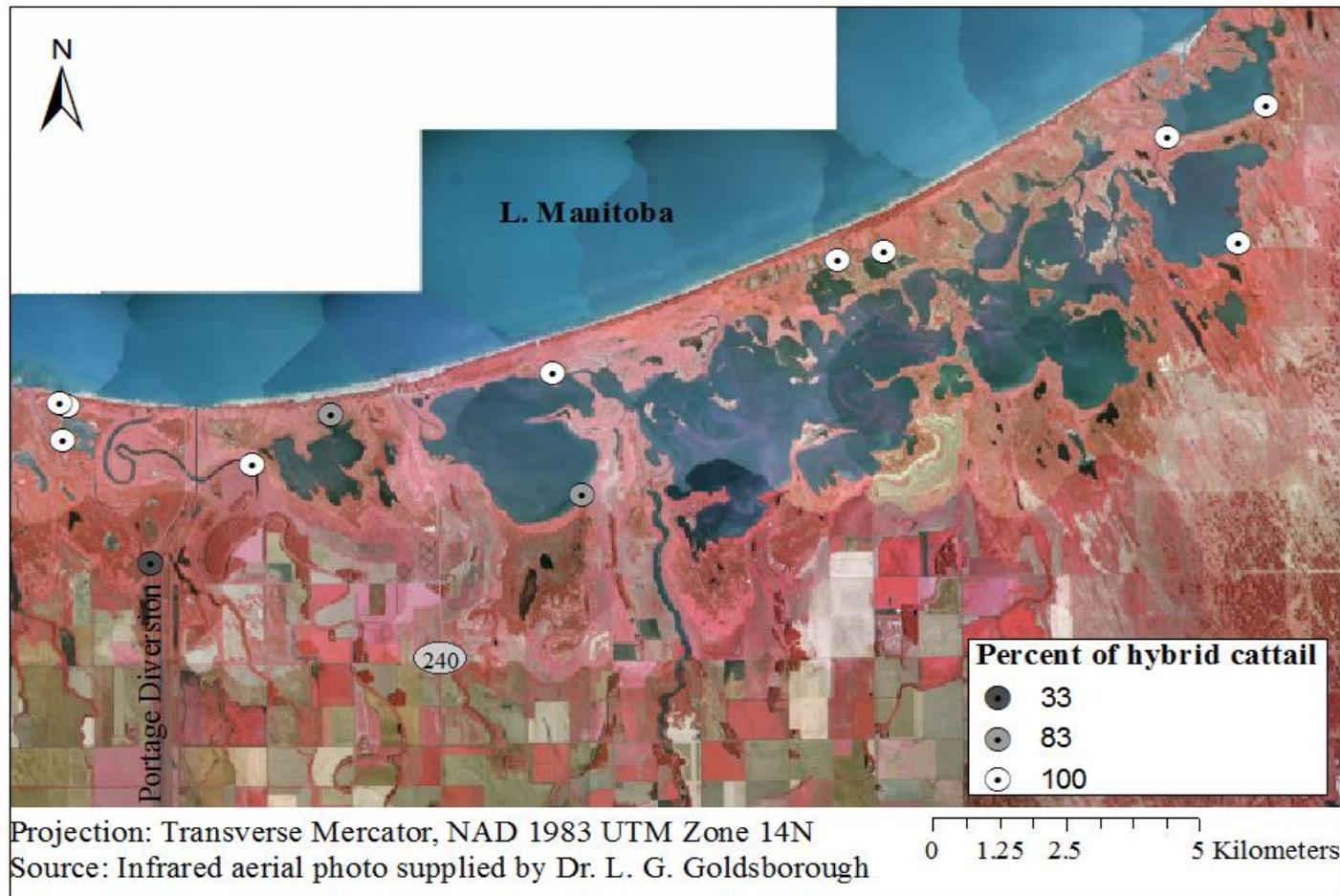


Fig. 2.1 The locations of thirteen transects sampled for cattail species at Delta Marsh, Manitoba, and the percent of hybrid cattail, *Typha x glauca*, identified at each transect, 2009. Base map infrared aerial photo courtesy of Dr. L. G. Goldsborough, University of Manitoba, 2003. See Appendix A for GPS locations of all transects

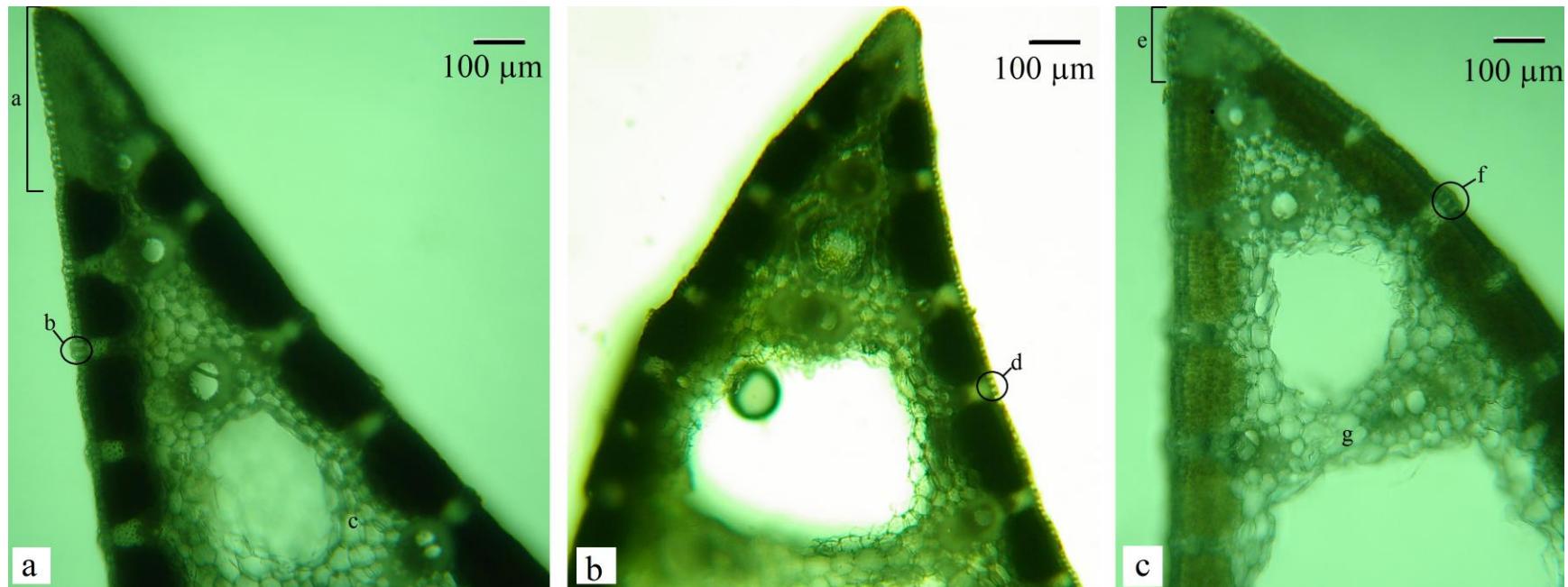


Fig. 2.2 Cattail leaf edge cross-sections viewed through a green filter. **a** *Typha latifolia*. Note the (a) oblong-shaped tip, (b) enlarged epidermal cells above the vascular bundles, and (c) more irregular arrangement of mesophyll cells. **b** *T. angustifolia*. Note the (d) absence of enlarged epidermal cells above vascular bundles. **c** *T. x glauca*. Note the (e) wedge-shaped tip, (f) enlarged epidermal cells above the vascular bundles, and the (g) I-beam arrangement of mesophyll cells

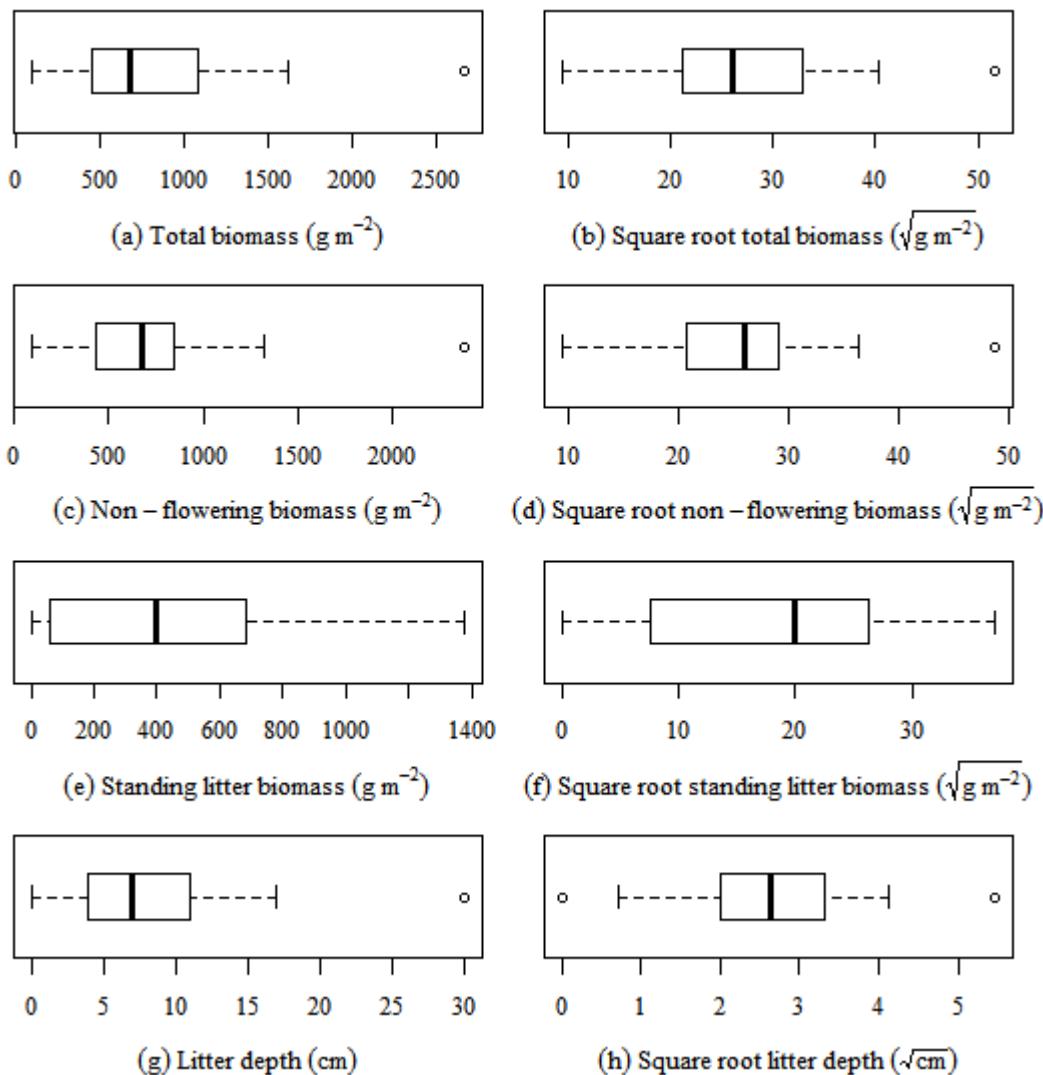


Fig. 2.3 Box and whisker plots of Delta Marsh total above-ground cattail biomass, non-flowering cattail biomass, cattail standing litter biomass, and litter depth on the left (a, c, e, and g) and their square root transformed counterparts on the right (b, d, f, and h). The boxes represent the range of values within the 25-75% percentiles, the ditto lines within the boxes represent the median values, the whiskers extend from the boxes to the minimum and maximum values, and the open circles represent potential outlier data

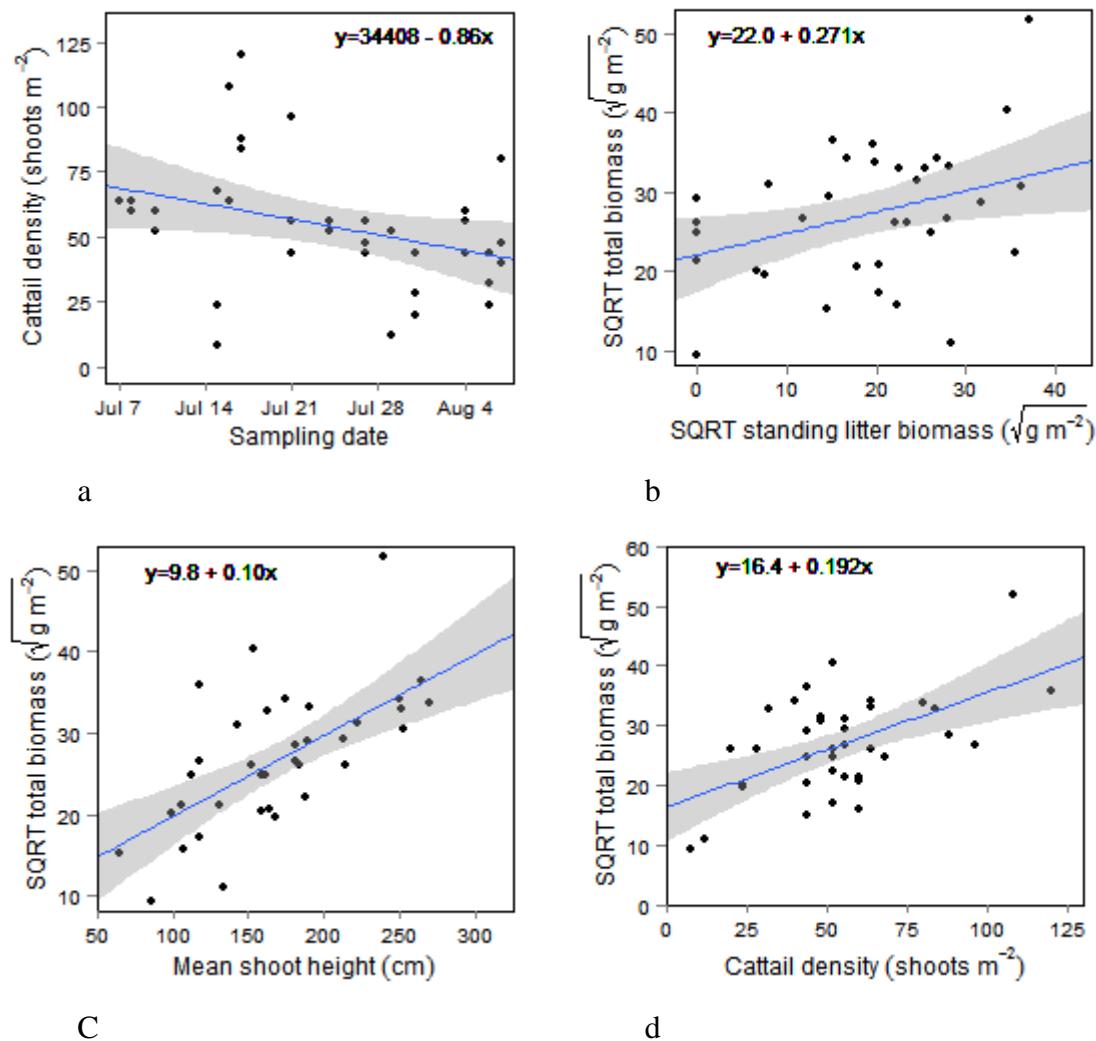


Fig. 2.4 Scatterplots of statistically significant results of ANOVA linear regression of all combinations of the following cattail variables: mean height, density, square root of above-ground biomass, square root of standing litter biomass, fallen litter biomass and square root of litter depth, n=37. **a** Sampling date versus density, **b** SQRT standing litter biomass versus SQRT above-ground biomass, **c** mean shoot height versus SQRT above-ground biomass, **d** cattail density versus SQRT above-ground biomass. The 95% confidence intervals are represented by the shaded areas around the lines of best fit. See fig. 2.5 for the remaining scatterplots

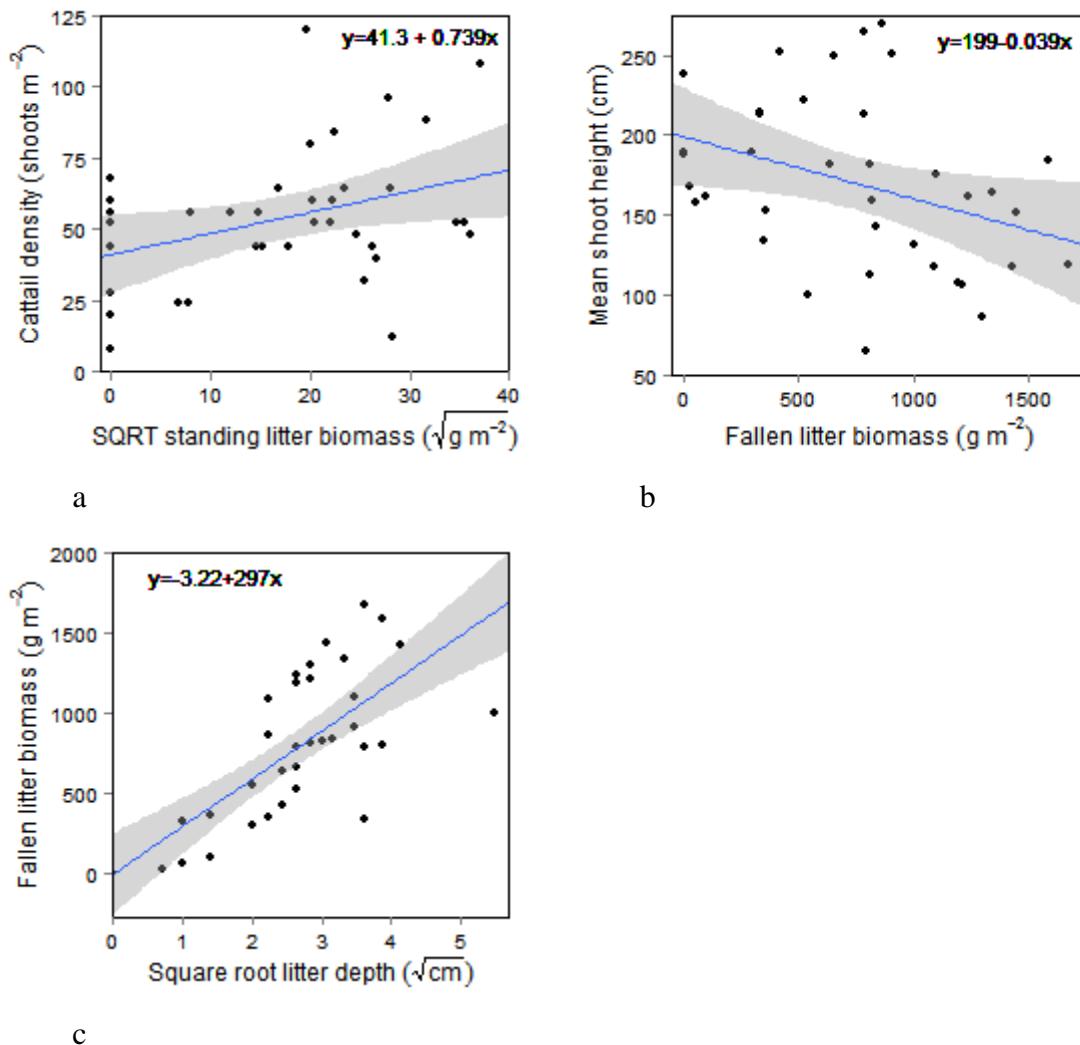


Fig. 2.5 Remaining scatterplots of statistically significant results of ANOVA linear regression of all combinations of the following cattail variables: mean height, density, square root of above-ground biomass, square root of standing litter biomass, fallen litter biomass and square root of litter depth, $n=37$. **a** SQRT of standing litter biomass versus cattail density, **b** fallen litter biomass versus mean cattail shoot height, **c** SQRT litter depth versus fallen litter biomass. The 95% confidence intervals are represented by the shaded areas around the lines of best fit. See fig. 2.4 for the rest of the scatterplots

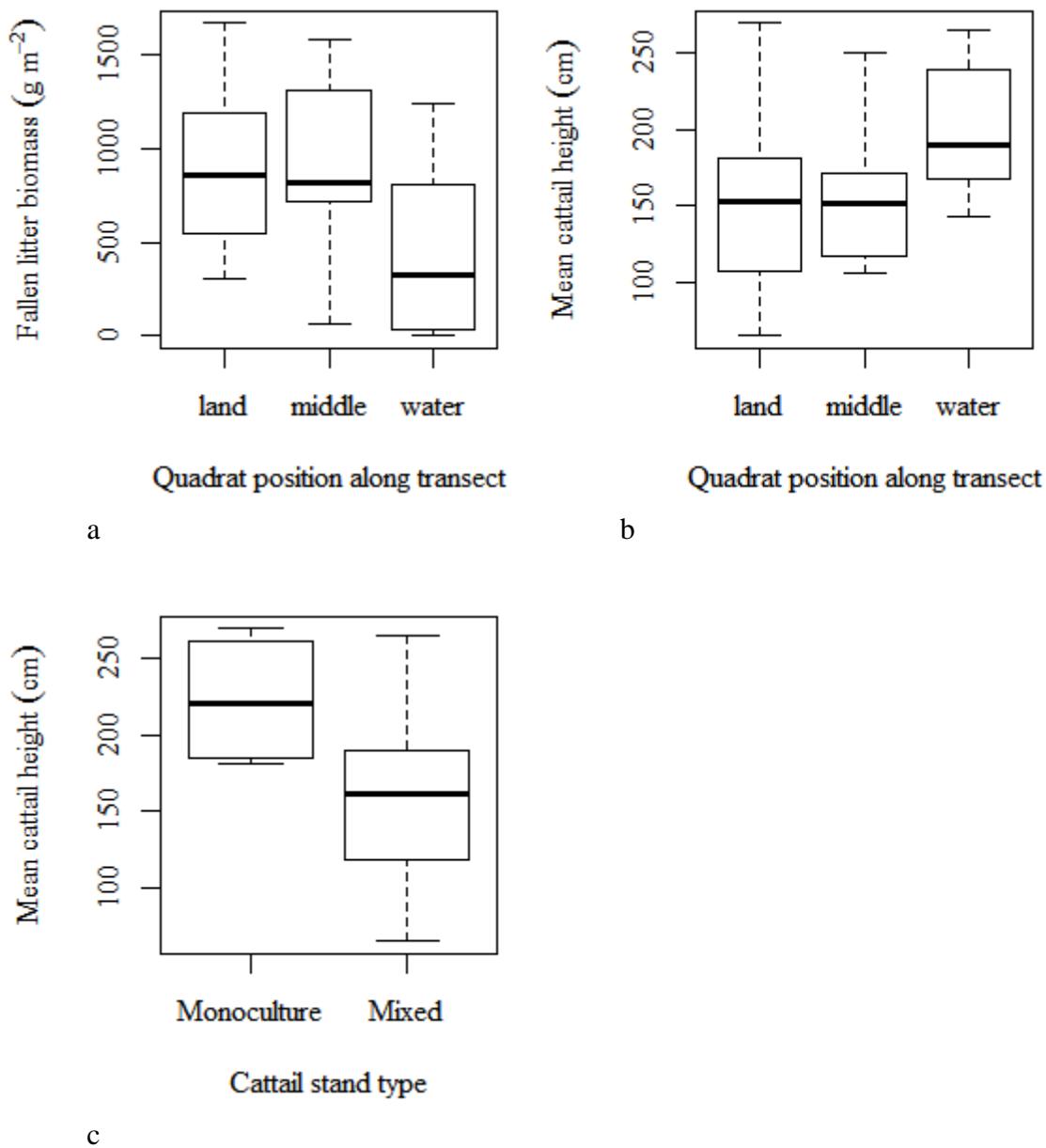


Fig. 2.6 Box and whisker plots of a cattail fallen litter biomass at the three relative positions of land edge, middle, and water's edge, b mean cattail height at the three relative positions along the transects, c mean cattail height of *T. x glauca* monoculture stands and stands with a mixture of *T. x glauca* and *T. angustifolia* along transects through cattail stands at Delta Marsh, n=37. The boxes represent the range of values within the 25-75% percentiles, the ditto lines within the boxes represent the median values, and the whiskers extend from the boxes to the minimum and maximum values

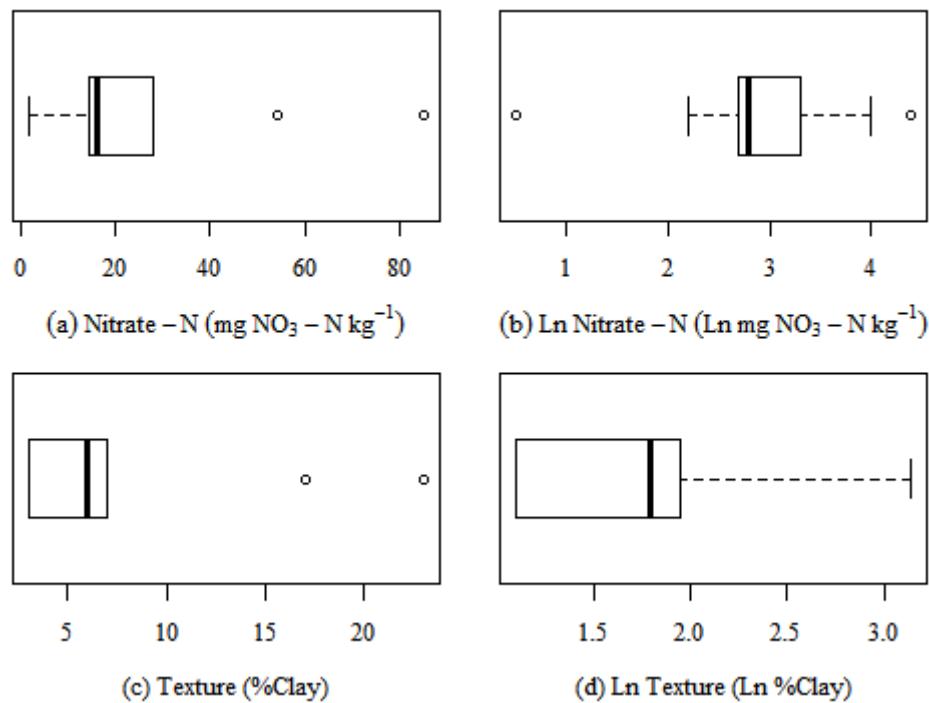


Fig. 2.7 Box and whisker plots of (a) sediment nitrate-N, (b) natural logarithmic transformed nitrate-N, (c) sediment texture, and (d) natural logarithmic transformed sediment texture, n=9. The boxes represent the range of values within the 25-75% percentiles, the ditto lines within the boxes represent the median values, the whiskers extend from the boxes to the minimum and maximum values, and the open circles represent potential outlier data

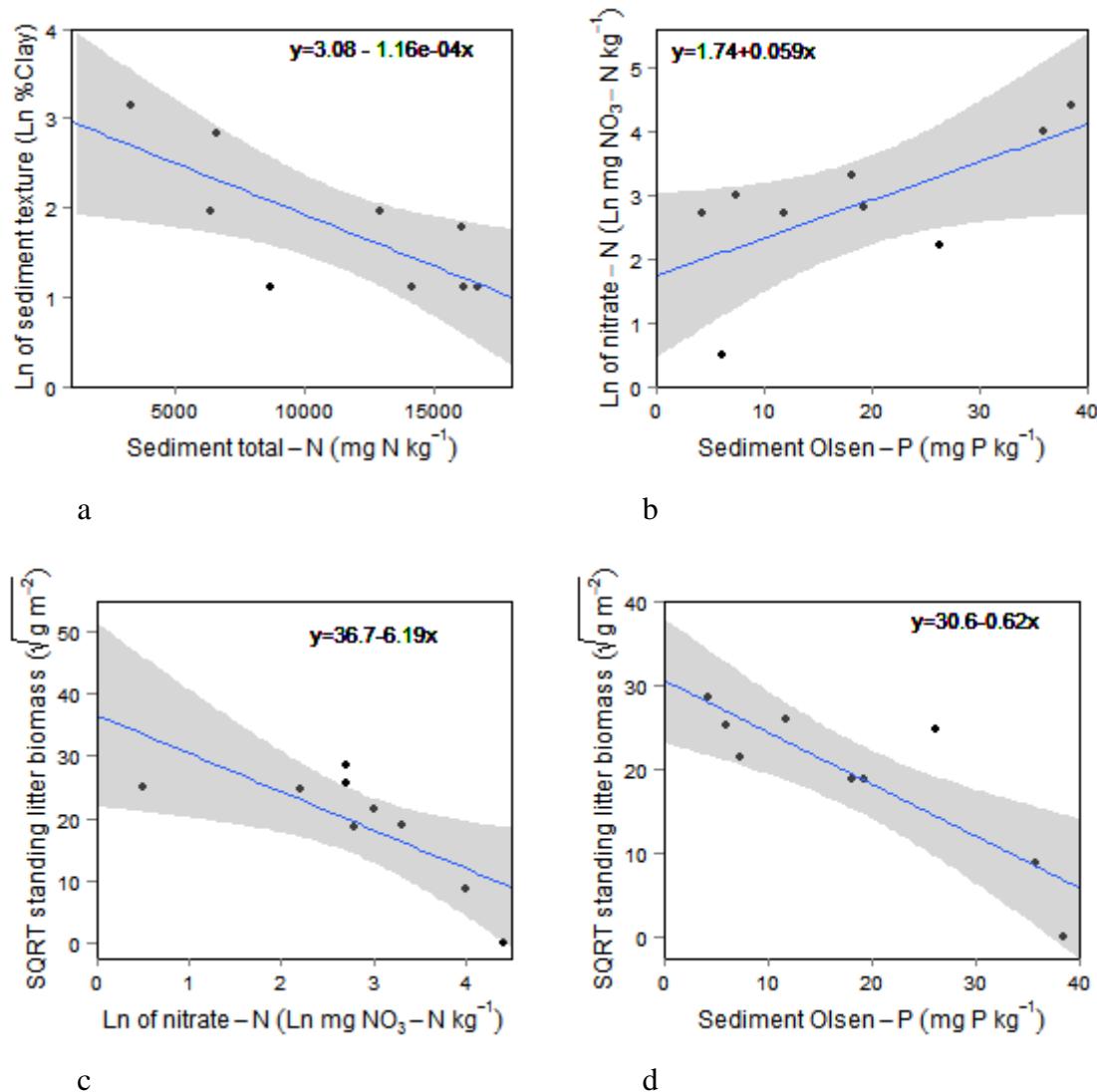


Fig. 2.8 Scatterplots of the statistically significant results of ANOVA linear regression of all combinations of the following variables: sampling date, transect length, water conductivity, sediment texture, total-N, nitrate-N, organic-C, and Olsen-P; the above listed variables each with the following variables: square root of above-ground biomass, fallen litter biomass, square root of standing litter biomass, and mean cattail shoot height, $n=9$. **a** total-N versus \ln of sediment texture, **b** Olsen-P versus \ln of nitrate-N, **c** \ln of nitrate-N versus SQRT standing litter biomass, **d** Olsen-P versus SQRT standing litter biomass. The 95% confidence intervals are represented by the shaded areas around the lines of best fit

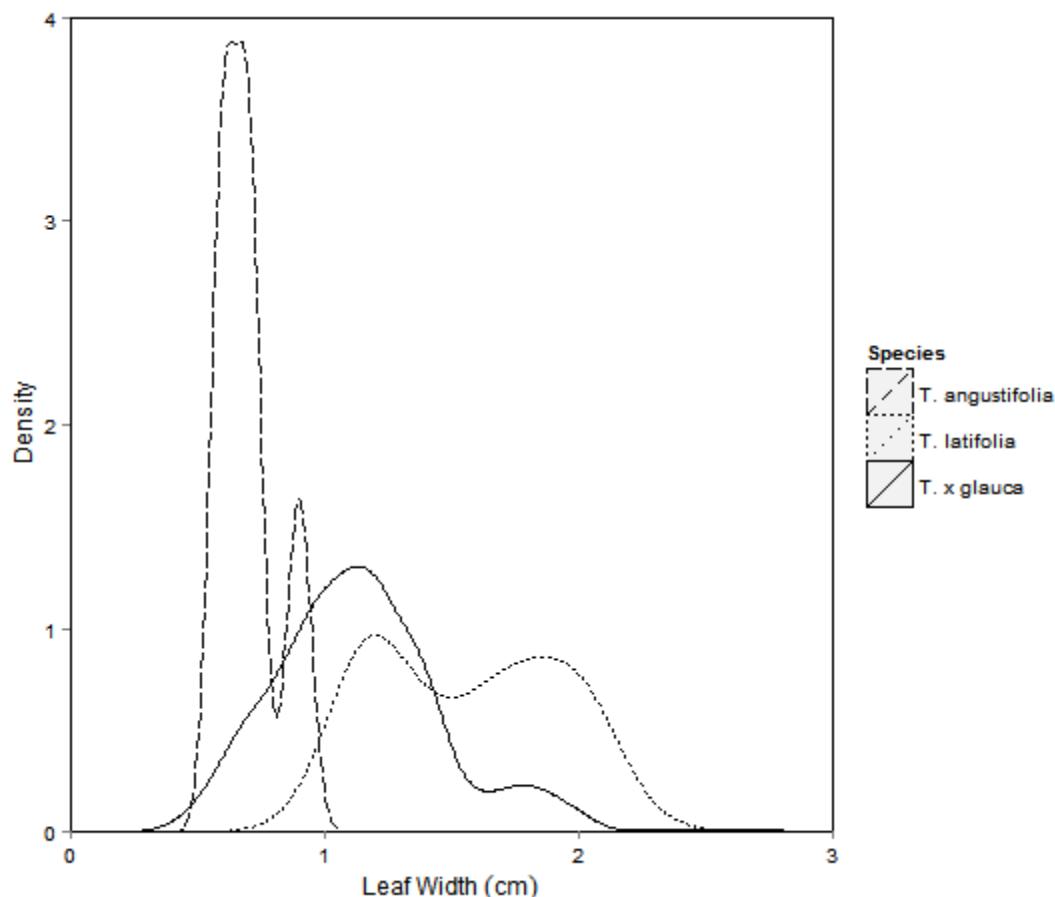


Fig. 2.9 Cumulative frequency distributions of leaf width for 80 *Typha latifolia*, 5 *T. angustifolia*, and 331 *T. x glauca*, collected in southwestern Manitoba and southeastern Saskatchewan prairie pothole, ditch, and lacustrine marshes in 2009 and 2011. The area under each curve is equal to 100% of the distribution sampled for each species. Specimens were identified with the leaf-lamina-margin method adapted from McManus et al. (2002). n = 416

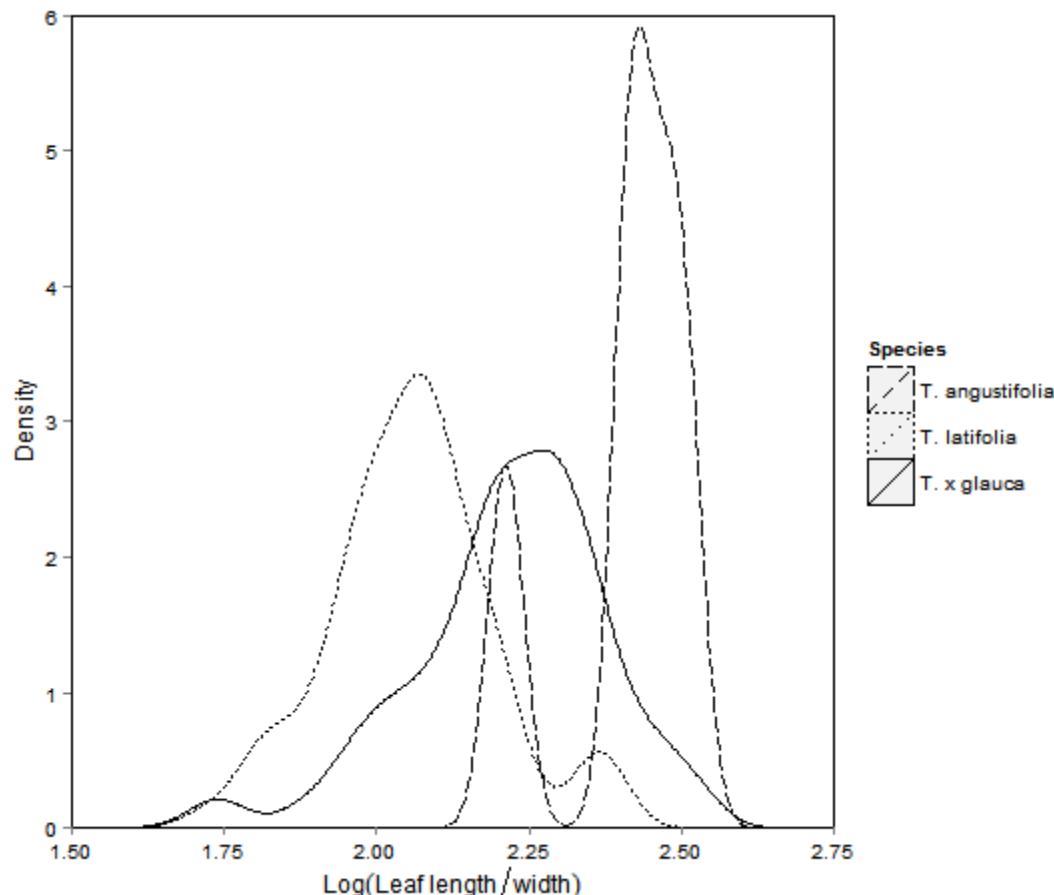


Fig. 2.10 Cumulative frequency distributions of the logarithm of leaf length/ leaf width for 80 *Typha latifolia*, 5 *T. angustifolia*, and 331 *T. x glauca*, collected in southwestern Manitoba and southeastern Saskatchewan prairie pothole, ditch, and lacustrine marshes in 2009 and 2011. The area under each curve is equal to 100% of the distribution sampled for each species. Specimens were identified with the leaf-lamina-margin method adapted from McManus et al. (2002). n = 416

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Chapter 3. The distributions of *Typha latifolia*, *T. angustifolia*, and *T. x glauca* and a generalized linear model of *T. x glauca* distribution and its environment within prairie potholes and ditches in southwestern Manitoba and southeastern Saskatchewan, 2011

Abstract

While the distributions are well documented in eastern North America for the cattail species *Typha latifolia*, *T. angustifolia*, and their hybrid, their distribution in western North America is largely unreported. The distribution of these cattail species and hybrid were surveyed in 2011 in prairie pothole and roadside ditch marshes across southwestern Manitoba and southeastern Saskatchewan. Plants were identified by analysis of microscopic leaf-lamina margin characteristics. *T. x glauca* was most widespread, followed by *T. latifolia*, whereas *T. angustifolia* was rare and only found as far west as central Manitoba. Current understanding of correlations between cattail invasions and their environment was conflicting and largely based on lacustrine wetland studies. A generalized linear model was developed which explained approximately 40% of the variation in *T. x glauca* distribution in the prairie potholes and ditches. The model included the environmental variables of sediment Olsen-P, sediment nitrate-N, water pH, litter depth, surrounding land use, and the interaction variable of Olsen-P:nitrate-N. Olsen-P was the most important of these variables, because its removal from the model significantly reduced the residual deviance of the model ($P=0.05$). GPSNorthing,

GPSEasting, sediment texture, sediment organic-C, sediment total-N, sediment ammonium-N, water conductivity, DOC in water, dissolved-N in water, transect length, and sampling date were dropped from the model because of collinearity with other variables, or because they did not significantly contribute to explaining hybrid cattail distribution.

Introduction

Cattails (*Typha* spp.) have become invasive in Canadian prairie wetlands, displacing sedge meadows, as well as invading open water and decreasing biodiversity (Grace and Harrison, 1986; Galatowitsch et al., 1999). Cattail expansion has been linked with anthropogenic disturbances such as urbanization and agricultural activities, which open up new sites for colonization. Of particular concern is the hybrid cattail, *T. x glauca*, although the parental species *T. latifolia* and *T. angustifolia* have been identified as potentially invasive as well (Galatowitsch et al., 1999). *T. x glauca* appears to be especially capable of taking advantage of disturbances, because it is particularly abundant following anthropogenic disturbances such as urban development, agricultural eutrophication, and hydrological alterations (Zedler and Kercher, 2004; Olson et al., 2009).

Cattail invasion may be dependent on local conditions, because different studies have reported conflicting results regarding the correlations between cattail expansion and environmental factors. Stabilized water levels in both natural and constructed wetlands in

Illinois (Boers et al., 2007) and throughout the prairie pothole region of North America (van der Valk, 2005) have been correlated with *T. x glauca* invasion. Stabilized water levels in combination with phosphorus additions contributed to the success of the hybrid at displacing native vegetation in riverine and lacustrine Wisconsin wetlands (Boers and Zedler, 2008). Urbanization has been linked to the expansion of *T. x glauca* in wetlands of the Great Lakes region that have retained their historical water level fluctuations (Frieswyck and Zedler, 2007). However, Vaccaro (2005) found that agriculture intensity was more important to cattail dominance than urbanization in the Great Lakes region. The persistent dominance of *Typha* spp. in a lacustrine Iowa marsh that retained its natural water level fluctuations was attributed to both eutrophication and the invasion of common carp (*Cyprinus carpio*), which have elevated nutrient levels, increased turbidity, and increased both sediment resuspension and disturbance (Egertson et al., 2004).

The deep litter layer deposited by cattails also facilitated further expansion by excluding other species through shading (Jordan et al., 1990; Vaccaro et al., 2009; Farrer and Goldberg, 2009). Freyman (2008) found that litter accumulation and the high nitrogen accumulation rate of *T. x glauca* facilitated the competitive displacement of native vegetation in Great Lakes lacustrine wetlands. Increased water levels, and N and P inputs, appear to have facilitated the encroachment of *T. latifolia* in a marl wetland in Virginia (Drohan et al., 2006). Soluble nutrients in the sediment including soluble ammonium, nitrate, and phosphate, as well as high soil organic matter, bacterial diversity, above-ground plant biomass, and litter were significantly greater and plant species diversity was lower in sites invaded by *T. x glauca* than in native plant zones in a coastal wetland on

Lake Huron (Angeloni et al., 2006). A study spanning three nutrient eco-regions in the northern United States found that the presence of *Typha* spp. in mature wetlands was positively correlated with low species richness and high ammonia concentrations in water, but not with water nitrate or phosphate, and not with soil N or P concentration (Craft et al., 2007). A study of Michigan riverine and pothole marshes found no correlation between the presence of the different cattail species or hybrid in riverine and marsh cattail stands to floristic diversity or to any of the following environmental variables: sediment texture, pH, available calcium, potassium, or available phosphorus (Segadas-Vianna, 1951). Bevington (2007) also found no differences between soil organic matter, total-P, or total-N in created wetlands in Virginia. Once established, *T. x glauca* was persistent and difficult to control. Boers et al. (2007), found that in order for a native plant restoration to be successful, *T. x glauca* must be completely removed from a site. If any hybrid cattail remains it rapidly invades areas seeded with native vegetation and is expected to out-compete the native flora over time.

Hybridization increases invasiveness by increasing genetic variability and phenotypic plasticity (Ciotir et al., 2013). Hybrid vigour and increased plasticity contribute to the invasiveness of *T. x glauca* (Ciotir et al., 2013). Phenotypic plasticity of *T. x glauca* has been well documented (Marsh, 1962; Grace and Harrison, 1986; Marcinko-Kuehn and White, 1999). Increased phenotypic plasticity has been linked to the successful invasion by several hybrid species (Ward et al., 2008). Phenotypic plasticity makes it difficult to draw conclusions from studies where cattail species and hybrid were identified using gross morphology. Cattail identification based on gross external morphology alone is

cryptic and inaccurate, because the hybrid can appear identical to either parent or as an intermediate between the two (Hotchkiss and Dozier, 1949; Fassett and Calhoun, 1952; Smith, 1967; Marcinko-Kuehn and White, 1999; Selbo and Snow, 2004).

T. latifolia is native to North America, whereas *T. angustifolia* is thought to be an introduced species from Europe that arrived in eastern North America around the time of European colonization (Ciotir et al., 2013). According to herbarium records, *T. latifolia* and *T. angustifolia* have been expanding their geographic ranges at similar rates since the mid-20th Century (Shih and Finkelstein, 2008). The hybrid cattail is capable of forming wherever the parent species are sympatric (Shih and Finkelstein, 2008). The range of *T. angustifolia* now extends at least as far west as central Manitoba, and *T. x glauca* has been reported as far west as Saskatchewan (Grace and Harrison, 1986; Galatowitsch et al., 1999; Shih and Finkelstein, 2008), although the western distribution of these two taxa has been largely unreported in the literature.

The objectives of this study were (1) to describe the distribution of *T. latifolia*, *T. angustifolia*, and *T. x glauca* in southwestern Manitoba, and southeastern Saskatchewan, and (2) to develop a multivariate model that describes the distribution of cattail species and hybrid in order to assess their association with the environmental variables of geographic location, fallen litter depth, surrounding land use, sediment texture and chemistry, and water quality.

Methods

Site selection

Study sites were located across southwestern Manitoba and southeastern Saskatchewan, in both prairie potholes and ditches within 150 km radii of the following urban centres: Killarney, Minnedosa, Russell, and Winnipeg. These centres were chosen for their convenience and geographic spread within the study region (Fig. 3.1). A map of the study sites was created using ArcGIS 9.3, and a basemap obtained from GeoGratis (Natural Resources Canada, 2013). Prairie pothole sites were selected by searching GoogleEarth satellite imagery within the predetermined radii. The only size criterion was that potholes had to be large enough to be visible on the satellite images. All sites were accessible by truck or required only a short walk from a nearby road. Ditch sites were chosen on the day of sampling by first going to the pothole site and then driving until a cattail stand was found in a nearby road ditch. There was no *a priori* knowledge about surrounding land use, date of cattail colonization, or date of marsh formation. All sampling took place from 27 June to 31 August 2011. Extensive flooding in 2011 throughout southern Manitoba and in the southeast region of Saskatchewan made some potential study areas inaccessible for this survey.

Field sampling

The *Typha* species have different water depth tolerances. Grace and Wetzel (1981) reported that *T. latifolia* was restricted to water depths less than 80 cm and obtained optimal growth at 50 cm, *T. angustifolia* was found growing in water depths up to 100 cm

with optimal growth at 50 cm. Waters and Shay (1992) reported *T. x glauca* in water depths up to 100 cm with optimal growth at 25 cm and 100 cm. Therefore, each sampling transect was oriented along the water depth gradient, starting at the landward edge of the cattail stand and extending to where the cattails met the open water. One leaf from each of six cattail ramets equidistant along each transect was collected for species identification. Because cattail stands vary in size, the transect lengths varied from 2 to 50 m. However, the number of specimens collected at each transect was constant. For ditches, I divided each transect in half and formed two transects, approximately 10 m apart. For each ditch half-transect, one specimen was collected at the bottom of the ditch and one from each bank. For each cattail leaf collected, I recorded both the leaf width, which was measured at the widest point of the leaf, and leaf length, which was measured from where the cattail emerges from the sediment to the tip of the tallest leaf.

To assess the abiotic characteristics of the sampling sites, environmental data were collected as described below. Water measurements and samples were collected from a point approximately 1 m from the cattail stand in open water: conductivity ($\mu\text{S cm}^{-1}$), pH, dissolved-N (mg-N L^{-1}), and dissolved organic-C (mg-DOC L^{-1}). If no open water was present at a site, samples were collected from the center of the cattail stand. Using a soil corer (Fig. 3.3), three cores of the top 10 cm of sediment were taken within 1 m of each leaf collection point and combined. Where standing water was present, I used my hand to cover the sediment so that it would not be lost as the core was retrieved. The water and sediment samples were transported on ice from the field to the laboratory where water samples were frozen. GPS location of each site was recorded in the UTM

coordinate system. Litter depth (cm) was reported as the mean of all of the litter depth readings along each transect. At each leaf collection point, five readings of litter depth (cm) were measured with a meter stick. Each litter depth reading was randomly taken within 1m of each leaf collection point.

Surrounding land use was categorized as crop, pasture/hay, or bush. Categories were assigned to each wetland based on what land use type was most dominant in the land that immediately surrounded the wetland. I combined pasture and hayland into the same category because it is sometimes difficult to distinguish between grassland that is not harvested but used only as pasture, and grassland that is used solely for harvesting hay, and grassland that is used both as pasture and as hay. I assumed that the fertilizer inputs on pasture and hay land were similar and that the fertilizer inputs were lower for pasture/hay than for crop land.

Species and hybrid identification

From each cattail ramet collected for identification, a 5-cm section of leaf was wrapped in wet paper towel, placed in a labeled plastic bag in the field, and transported on ice to the laboratory. Semi-permanent mounts of the leaf cross-sections in thymol-glycerin media were prepared with a hand-held razor blade on the same day of collection. The thymol-glycerin media was prepared with 75% glycerin to 25% water with a few thymol crystals added and dissolved as a preservative (Zander, 1997). The coverslip was sealed at the edges with clear nail polish to prevent desiccation. In addition, one 15-cm section of leaf from each specimen was cut into three 5-cm sections, air-dried in a leaf press, and

stored in silica gel to allow for future genetic analysis. These leaf samples will be stored at University of Manitoba, Department of Biological Sciences until they have been analyzed.

The following four leaf-lamina-margin characters, adapted from McManus et al. (2002), were used to identify cattails to species are: (1) the general shape of the leaf edge, recorded as one of two categories: (i) oblong, or (ii) wedge; (2) the number of vascular bundles per leaf cross section within the zone of fibers near the leaf edge; (3) the presence or absence of thickened epidermal cells above the vascular bundles; and (4) the arrangement of the mesophyll cells connecting the adaxial and abaxial leaf surfaces, recorded as one of two categories: (i) mesophyll cells arranged in I-beam formation, or (ii) mesophyll cells arranged in a loose arch (Table 3.1, Fig. 3.2). The leaf cross-sections were viewed through a compound microscope at magnifications of 100 x and 400 x. A green filter was used to increase the contrast so that staining was not required. Pictures of all leaf cross-sections were taken with a microscope-mounted camera.

Sediment analysis

A 5-g subsample from each sediment sample was dried at 105°C to determine the moisture content, to correct all sediment analyses results for moisture. All extractions were filtered with Whatman No. 42 filter papers prior to analysis.

To extract nitrate-N from the sediment, 50 mL of 2N potassium chloride and 10 g of field-moist sediment from each sample was shaken at 120 rpm for two hours and then filtered (Mulvaney, 1996). The extract was stored frozen prior to analysis for nitrate-N

concentration ($\text{mg NO}_3\text{-N kg}^{-1}$ dry sediment) and ammonium-N concentration ($\text{NH}_4\text{-N kg}^{-1}$ dry sediment). Micro-segmented air flow analysis used an Astoria 2 spectrophotometer and the cadmium and phenate reduction methods for nitrate-N and ammonium-N, respectively (Mulvaney, 1996). The detection limits were 0.01-5.00 $\text{mg NO}_3\text{-N L}^{-1}$ and 0.05-25.0 $\text{mg NH}_4\text{-N L}^{-1}$. For each run, the cadmium reactor nitrate reduction efficiency was checked prior to analysis. Samples were analyzed only if the efficiency was between 90 and 110%. Two replicates were analyzed for each sample, and a low-level standard was run every 30 samples. Nitrate-N replicates had an average standard deviation of 1.74 $\text{mg NO}_3\text{-N kg}^{-1}$ dry sediment and ammonium-N replicates had an average standard deviation of 9.09 $\text{mg NH}_4\text{-N kg}^{-1}$ dry sediment. Calibration standards (Appendix B) were prepared with the same matrix as the samples. The results were corrected for baseline drift, blanks, carryover, and moisture content. Results were converted from $\text{mg NO}_3\text{-N L}^{-1}$ extraction and $\text{mg NH}_4\text{-N L}^{-1}$ extraction to $\text{mg NO}_3\text{-N kg}^{-1}$ dry sediment and $\text{mg NH}_4\text{-N kg}^{-1}$ dry sediment, respectively.

The remaining sediment sample was air-dried, pooled by site, and crushed to pass through a 2-mm sieve prior to further analysis. The hydrometer method was used to determine sediment texture (Carter, 1993). After passing the sediment through a 0.4-mm sieve, the loss-on-ignition method was used to determine the organic matter concentration (mg OM kg^{-1} dry sediment) which was then converted to organic-C concentration ($\text{mg organic-C kg}^{-1}$ dry sediment) (Nelson and Sommers, 1996).

To extract phosphorus from the air-dried and screened sediment, 2.5 g of sediment with 50 mL of 0.5 M sodium bicarbonate, adjusted to pH 8.5 with sodium hydroxide, was

shaken at 120 rpm for two hours and then filtered. The extract was refrigerated prior to analysis for Olsen-P concentration (mg P kg^{-1} dry sediment) and total sodium bicarbonate extractable P concentration, hereafter referred to as total-P (mg P kg^{-1} dry sediment) (Kuo, 1996). The detection limit was 0.5-10.0 mg P L^{-1} for these methods. The samples were adjusted to pH 6 with additions of concentrated HCl prior to spectrophotometric analysis.

The P extractant colour ranged from clear to dark brown. The absorbency spectrum of a subsample of light and dark coloured samples were checked with a spectrophotometer which confirmed that at least some of the samples absorbed light at 660 nm, the primary wavelength where P quantification was done. This would result in some overestimation of Olsen-P concentration. I re-ran all of the samples using a modified method where distilled water replaced the molybdenum (IV) and antimony (III) reagent. The absorbance readings of each sample without colour reagent were used as blanks for the corresponding Olsen-P analyzed samples. Two replicates were analyzed and a low-level standard was run every 30 samples. Olsen-P analysis replicates had an average standard deviation of $0.17 \text{ mg P kg}^{-1}$. Concentrated HNO_3 was added to the samples to produce a 2% nitrate solution prior to analysis for total P using inductively coupled plasma mass spectrometry (ICP). For total P, detected at the 177.434 nm wavelength, three replicates were sampled. Total-P replicates had an average standard deviation of $1.03 \text{ mg P kg}^{-1}$. Calibration standards (Appendix B) were prepared with the same matrix as the samples. Results were corrected for moisture content and for the dilutions. Results were converted from mg P L^{-1} extraction to mg P kg^{-1} dry sediment.

Olsen-P is a frequently used measurement for soil phosphorus, which measures the sodium bicarbonate extractable inorganic phosphorus available in the soil as orthophosphate. The ICP measures the total sodium bicarbonate extractable phosphorus available, consisting of both inorganic P, organic P, and colloidal P. Thus I would expect that the ICP-measured total-P would always be equivalent or higher than the Olsen-P inorganic phosphorus. However, 12 out of 58 samples had lower total-P values than Olsen-P values, with the difference of total-P minus Olsen-P ranging from -1.6 to -28.4 mg P kg⁻¹ dry sediment. For eight of these 12 samples, the difference was small enough that the discrepancy may be due to variability inherent in the methodologies, with the numbers within the margin of error allowed by standard deviation. However, the remaining five samples cannot be explained by the combined standard deviations. A thorough methodological study is required to decipher whether total-P or Olsen-P was the more appropriate test for assessing phosphorus in cattail marsh sediments. This evaluation is beyond the scope of the present study. Interference of some form was assumed for some of the ICP analyses, and all phosphorus measurements reported and discussed were the more widely used spectrophotometric form of Olsen-P values.

Sediment passed through a 1-mm sieve was analyzed for total C concentration (mg C kg⁻¹ dry sediment) (Skjemstad and Baldock, 2008) and total N concentration (mg N kg⁻¹ dry sediment) (Rutherford et al., 2008) by combustion using a Leco Tru-Spec analyzer. Samples were corrected for atmospheric moisture (0.04 %). At the beginning and end of each analysis day, blanks and EDTA standards (Appendix B) were run to verify consistent and accurate results and two replicates of each sample were analyzed. The

average standard deviation of replicates for total C and total N were $1468 \text{ mg C kg}^{-1}$ and $156.3 \text{ mg N kg}^{-1}$, respectively. Twelve of the 39 sediment samples analyzed had higher results for organic-C than for total C. Total C was removed from further analysis in favor of the more widely used organic-C values.

Water analysis

Water samples were transported on ice from the field to the laboratory, where they were kept refrigerated at 4°C before analysis. Prior to analysis, samples were centrifuged at 3000 rpm for 20 minutes and the supernatant was passed through a $0.45\text{-}\mu\text{m}$ millipore filter. Total dissolved organic-C (DOC) concentration (mg L^{-1}) and total dissolved N (DN) concentration (mg L^{-1}) were analyzed with the combustion catalytic oxidation method using a Shimadzu analyzer with two replicates per analysis (Shimadzu, 2014). The average standard deviation of the DOC replicates was 0.6430 mg L^{-1} and the average standard deviation of the DN replicates was 0.7894 mg L^{-1} .

Statistical analysis

All sites with no water were removed to avoid uneven dataset sizes when comparing models. This omission should also minimize sediment nutrient differences due to the wetlands being in different aerobic stages. Because there were no wetlands without water included in the analysis, the majority of sediment samples analyzed should have been from anaerobic sediments. Only one site, a ditch marsh near Glenboro, MB, contained *T. angustifolia*, which could not be statistically analyzed, so it was removed from the

dataset. The total number of pothole and ditch sites analyzed were 23 and 16, respectively, for a total of 39 sites.

To reduce the effects of their skewed distributions, natural logarithmic transformation was used for the sediment variables total-N and ammonium, for the water column variables total dissolved N (DN), dissolved organic-C (DOC), and conductivity, as well as transect length (Fig. 3.4). Models of the *T. x glauca* distribution had the following potential continuous predictor variables: GPSNorthing, GPSEasting, Ln of transect length, sediment texture, sediment Olsen-P, the Ln of sediment total-N, the Ln of sediment nitrate-N, the Ln of sediment ammonium-N, sediment organic-C, water pH, the Ln of water conductivity, the Ln of DOC in water, and the Ln of DN in water; and the factor variable of land use with the following three factor levels: crop, pasture/hay, and bush. The mean, standard deviation, and coefficient of variation were calculated for each continuous predictor variable prior to transformations.

After confirming that the continuous predictor variables between the pothole and ditch marsh types were not significantly different ($P=0.081$) with a two-sample Hotelling T^2 test, the data from the potholes and ditches were combined to increase sample size (Timm, 2002). For the Hotelling T^2 test, GPS location was removed from the analysis because GPSNorthing and GPSEasting were similar for the ditch and pothole sites due to sampling design. The inclusion of the GPS locations would have biased the results of the Hotelling T^2 test.

I tested for correlations between all combinations of the continuous predictor variables with ANOVA linear regression ($P=0.05$). Autocorrelation was prevented by omitting one

of the variables wherever there was a correlation between two predictor variables.

Variance inflation factor (VIF) of candidate models was calculated to test for collinearity between predictor variables where a VIF greater than 10 indicated potential collinearity (Quinn and Keough, 2002).

Simple logistic regression was used to investigate relationships between *T. x glauca* proportion and each predictor variable. Generalized linear model (GLM) logistic regression was used for model formation with multiple predictor variables. Because the data were overdispersed with a dispersion factor of 2.8, a quasibinomial logistic regression with the logit link function was chosen. The full model was selected using a backward step procedure (Zuur et al., 2009), where all potential predictor variables that were free from collinearity were included in a model. Analysis of deviance of that model revealed the variable that contributed the least to explaining the *T. x glauca* distribution and this variable was then removed. Variables were dropped one at a time using this criteria until the Full model was significantly better than the Null model at the P=0.05 significance level. The predictor variables within the Full model were recombined to produce all possible nested models. Next, sequential F-tests of the nested models were used to compare potential models at the P=0.05 significance level. Once the best model from the nested and Full model was selected, each term that had been previously omitted was added back into the model and compared to the best model with the analysis of deviance F-test. This last step was done to ensure that no significant terms had been dropped erroneously, due to the backward step procedure or due to choices made when selecting between correlated variables.

Potential interactions between variables were checked with the add1 function of the R package Stats v. 2.15.1, with the F-test option selected. Significant interaction terms were added to the Full model to produce a Full model with interaction terms (FI model). FI model was tested with analysis of deviance against both the Null and Full models at the P=0.05 significance level. A series of all of the possible nested models was produced from the FI model, where all parent terms of the interaction term were always retained. I tested all of the nested models against the FI model with analysis of deviance at the P=0.05 significance level.

The best model was selected with the criteria that the best model must be significantly better than the Null model and have the highest percent explained deviance of all candidate models. Percent deviance explained was calculated with the following formula: $100 \times (\text{null deviance} - \text{residual deviance})/\text{null deviance}$ (Zuur et al., 2009). Term plots, where the partial residual of each term was plotted against the term's values, were used to visualize what effect each term of the model had on the hybrid cattail distribution. The following diagnostics of the best model(s) selected were used to verify whether the final model was a good fit for the data. Influence of observations was checked with *Dfbeta* and residual plots. *Dfbeta* measures the standardized change in the estimated logistic regression coefficient when an observation is observed (Quinn and Keough, 2002). Goodness of fit of candidate models was checked by plotting observed versus predicted *T. x glauca* proportions (Zuur et al., 2009; Quinn and Keough, 2002).

All statistics were performed with the software RStudio v. 0.97.311, libraries car, Hotelling, and ggplot2 (R Core Team, 2012; Fox and Weisberg 2011; Curran, 2011, Wickham, 2009). The code used for analysis with RStudio can be found in Appendix D.

Results

T. x glauca was present throughout the study area which extended as far north as Dauphin, MB, south to the Canada-United States border, west to Yorkton, SK and east to St. Anne, MB (Fig. 3.1). For the GPS coordinates of all transects, see Appendix A. The proportion of cattails identified as the hybrid at each marsh was similar between the pothole and ditch marsh types (Fig. 3.5). Eighteen sites contained 100% *T. x glauca* and 0% *T. latifolia*, eight sites contained 83% *T. x glauca* and 17% *T. latifolia*, three sites contained 50% *T. x glauca* and 50% *T. latifolia*, two sites contained 17% *T. x glauca* and 83% *T. latifolia*, and only two sites contained 0% *T. x glauca* and 100% *T. latifolia* (Table 3.2).

The marshes ranged from dense cattail monocultures to heterogenous mixtures of cattail and other emergent plant species (Fig. 3.6, 3.7). The environmental variable with the lowest variability was water pH, with a coefficient variation (CV) of 6.7%. The CV of all other variables ranged from 44.3 to 197.2% (Table 3.3).

ANOVA linear regression revealed the following correlations between the predictor variables: GPS easting was correlated with both sediment texture ($P=0.027$, $r^2=0.126$) and the Ln of sediment ammonium-N ($P=0.004$, $r^2=0.201$); GPSNorthing was correlated with both the Ln of water conductivity ($P=0.002$, $r^2=0.231$) and the Ln of DOC in water

($P=0.019$, $r^2=0.140$); the Ln of transect length was correlated with the Ln of DOC in water ($P=0.027$, $r^2=0.125$), the Ln of sediment total-N ($P=0.020$, $r^2=0.138$), sediment nitrate-N ($P=0.048$, $r^2=0.102$), and sediment organic-C ($P=0.011$, $r^2=0.161$); the Ln of water conductivity was correlated with both the Ln of DN in water ($P=0.034$, $r^2=0.116$) and the Ln of DOC in water ($P=2.66e^{-04}$, $r^2=0.305$); the Ln of DN in water was correlated with the Ln of DOC in water ($P=1.02e^{-08}$, $r^2=0.593$); sediment texture was correlated with the Ln of ammonium-N ($P=0.011$, $r^2=0.162$); sediment Olsen-P was correlated with the Ln of sediment total-N ($P=0.024$, $r^2=0.130$); the Ln of sediment total-N was correlated with both the Ln of sediment ammonium-N ($P=0.002$, $r^2=0.238$), and sediment organic-C ($P=3.93e^{-09}$, $r^2=0.613$); the Ln of sediment ammonium-N was correlated with sediment organic-C ($P=0.003$, $r^2=0.220$); and sediment nitrate-N was correlated with sediment organic-C ($P=0.031$, $r^2=0.120$) (Table 3.4, Fig.3.8). Both the logarithm of transect length and sediment organic-C were removed because they were both correlated with several other variables. The logarithm of water DN was removed because it was strongly correlated ($r^2=0.593$) with the logarithm of DOC and the DN data still contained potential outliers after being transformed (Fig. 3.4). Because ammonium-N is the preferred N-source for cattails (Brix et al., 2002), the logarithm of sediment ammonium-N was retained and the logarithm of sediment total-N was omitted. The logarithm of water DOC was retained and the logarithm of water conductivity was omitted. Both GPSEasting and GPSNorthing were omitted to remove the remaining correlations between predictor variables.

Analysis of deviance between all quasi-binomial GLM models with one predictor variable and the null model revealed that Olsen-P was the only predictor variable that was significant by itself ($P=0.010$) (Table 3.5, Fig. 3.9). The Olsen-P model accounted for 15.1% of the *T. x glauca* distribution.

After the removal of the above-listed correlated predictor variables, the potential full model (P1) was written as follows:

$Y_i \sim B(n_i, \pi_i)$, where Y_i was the number of cattails identified as *T. x glauca* at site i and n was the number of cattails sampled. The β in the following formula represents the coefficients of the intercept and each variable.

$$E(Y_i) = \pi_i \times n_i \text{ and } \text{Var}(Y_i) = \phi \times n_i \times \pi_i \times (1 - \pi_i)$$

$$\text{logit}(\pi_i) = \beta_0 + \beta_1 \text{Texture} + \beta_2 \text{Ammonium-NLn} + \beta_3 \text{Nitrate-N} + \beta_4 \text{OlsenP} + \beta_5 \text{DOCLn} + \beta_6 \text{pH} + \beta_7 \text{Date} + \beta_8 \text{Litter} + \beta_9 \text{LandUse}$$

An analysis of deviance F-test revealed that this model was not significantly better than the null model ($P=0.264$). Collinearity of predictor variables was not suspected because the variance inflation factor of all variables were under 10, ranging from 1.0 to 2.3.

Analysis of deviance of the P1 model, where terms were added sequentially from first to last, revealed that the Ln of DOC in water contributed the least to the model with the smallest change in deviance of 0.57 (Table 3.6). The Ln of DOC in water was removed from P1 to produce the P2 model. The remaining potential full model (P2) was still not significantly different from the null model ($P=0.213$). Analysis of deviance of the P2 model revealed that Ln of sediment ammonium-N contributed the least with a change in

deviance of 0.60 (Table 3.7). The Ln of sediment ammonium-N was removed from P2 to produce the P3 model. The remaining potential full model (P3) was not significantly better than the null model ($P=0.206$). Analysis of deviance of the P3 model revealed that sediment texture contributed the least with a change in deviance of 0.92 (Table 3.8). Sediment texture was removed from P3 to produce the P4 model. The remaining potential full model (P4) was not significantly better than the null model ($P=0.113$). Analysis of deviance of the P4 model revealed that sampling date contributed the least with a change in deviance of 2.01 (Table 3.9). Sampling date was removed from P4 to produce the P5 model. The remaining potential full model (P5) was not significantly better than the null model ($P=0.071$). Analysis of deviance of the P5 model revealed that land use contributed the least with a change in deviance of 2.77 (Table 3.10), so it was removed. The remaining potential full model (P6) was significantly better than the null model ($P=0.031$), with an explained deviance of 26.6%. The add1 function of the Stats R package revealed that there was a significant interaction between sediment Olsen-P and sediment nitrate-N ($P=0.046$). In the P5 model, nitrate-N had contributed to the model with only a 3.65 change in deviance and therefore was the variable that contributed the least to the model after land use (Table 3.10). To remove the interaction, I took the P6 model and replaced nitrate-N with land use to form model P7. Analysis of deviance revealed that P7 was significantly better than the Null model ($P=0.036$), with an explained deviance of 28.4% (Table 3.11, Fig. 3.9). The add1 function revealed that there were no significant interactions between the predictor variables in model P7 at the $P=0.05$

significance level. Therefore, P7 was chosen as the Full model, hereafter referred to as the Full model.

Full model was written as follows:

$$\text{logit}(\pi_i) = \beta_0 + \beta_4 \text{OlsenP} + \beta_6 \text{pH} + \beta_8 \text{Litter} + \beta_9 \text{LandUse}$$

Analysis of deviance between each nested model with the Full model revealed that M8 and M9 were both worse models ($P=0.011$; $P=0.013$) (Table 3.12). No other models were significantly different from the Full model at the $P=0.05$ significance level. Out of all of the models formed by adding one previously deleted term to the Full model, no models were significantly different from the Full model at the $P=0.05$ significance level (Table 3.13).

Because there was an interaction between Olsen-P and nitrate-N, I took the Full model and replaced Olsen-P with nitrate-N and tested this model (M20) against the Null model. M20 was not significantly better than the Null model ($P=0.289$).

I then took the Full model and added the interaction term, nitrate-N:OlsenP, and its parent term, nitrate-N to produce the Full model with interactions (FI). Collinearity between variables was not a concern because the variance inflation factor for all variables, including those involved in the interaction, were between 1.0 and 3.8. Analysis of deviance revealed that the FI model was significantly better than the Null model ($P=0.040$), but was similar to the Full model ($P=0.152$) (Fig. 3.9). The FI model was written as follows:

$$\text{logit}(\pi_i) = \beta_0 + \beta_3\text{Nitrate} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_3\text{Nitrate}:\beta_4\text{OlsenP}$$

None of the nested models produced from the FI model were significantly different from the FI model at the P=0.05 significance level (Table 3.14).

The best model of all candidate models tested was the FI model. The difference in deviance between the Null and FI models was 50.15. The model approximately followed an F distribution with 7 degrees of freedom (P=0.040), and had an explained deviance of 37.2% (Table 3.11). Because term plots cannot be created for models with interaction terms and the Full model was equivalent to the FI model, I created term plots for the Full model to visualize the approximate effect that each term had on the hybrid cattail distribution. The proportion of *T. x glauca* decreased with increasing Olsen-P, increased with increasing pH, increased with increasing litter, and was greatest where the surrounding land use was crop land (Fig. 3.10). No influential points were revealed by the dfbeta plots for the FI model (Fig. 3.11). No outliers or trends were noticeable in the residual plots of the FI model (Fig. 3.12). Plotting the values for *T. x glauca* distribution fitted with the FI model against the observed distribution demonstrated that the FI model was a poor fit because most points lay outside of the 95% confidence band and the relationship, while approaching linear, did not extend from zero to one as expected (Fig. 3.9).

Discussion

The cattail ranges observed in this study agree with the ranges previously reported (Grace and Harrison, 1986; Shih and Finkelstein, 2008) although *T. angustifolia* was reported in Saskatchewan as early as 1986 (Galatowitsch et al., 1999). This study took place over the course of one season, and it was unknown whether the hybrid was displacing the native *T. latifolia* or whether it was expanding into wetlands that previously had no cattails. Further study is required to assess what the western and northern geographic limits of distribution are for the cattail species and hybrid. Documenting the rate of expansion in this area would be useful for characterizing and predicting the cattail invasion in the northern prairie pothole region.

The high variability of the environmental parameters of the cattail marshes sampled in this study was in accordance with previous studies which concluded that cattails are adaptable and can be found in both eutrophic and oligotrophic habitats (Bedford et al., 1999; Farrer and Goldberg, 2009). In particular, *T. x glauca* has been reported in widely varying habitats and part of its success has been attributed to its phenotypic plasticity and hybrid vigour which have enabled it to colonize habitats that were unavailable to *T. latifolia* and *T. angustifolia* (Ciotir et al., 2013).

The best model for describing the distribution of *T. x glauca* was the FI model which included sediment Olsen-P, sediment nitrate-N, litter depth, surrounding land use, and the interaction term of nitrate-N:Olsen-P. This model only explained approximately 40% of the data and was therefore not very useful for making predictions about the hybrid distribution based on the environmental variables within the model. The remaining 60%

may have been from one or more missing variables, or from chance distribution.

However, the Full model was equivalent to the FI model, and it explained less than 30% of the variation. When the *T. x glauca* distribution was plotted against the *T. x glauca* distribution predicted by each model, the majority of points were outside of the 95% confidence intervals. Therefore, both the FI model and the Full model were poor fits of the data.

The FI model is useful in highlighting which environmental variables with which the hybrid was most closely associated. The only predictor variable that was statistically significant on its own, was sediment Olsen-P. Olsen-P accounted for approximately 15% of hybrid cattail distribution variability. Sediment nitrate-N was an important variable only as an interaction variable between nitrate-N and Olsen-P. The term plots of the Full model revealed that the proportion of *T. x glauca* decreased with increasing Olsen-P. Therefore, *T. latifolia* increased with increasing Olsen-P. *T. x glauca* may be capable of luxury uptake of nutrients (Waters and Shay, 1990), which would enable it to survive in areas with fluctuating nutrient levels.

Beneficial associations between cattails and microbes may enable cattails to thrive in oligotrophic conditions or where nutrient availability fluctuates. *T. latifolia* was colonized by arbuscular mychorrizal (AM) fungi during flooding and drawdown events in Idaho (Ray and Inoue, 2005) and Florida (Ipsilantis and Silvia, 2007). Such associations with AM fungi may increase the P available to cattails, enabling cattails to survive in low-P environments. Likewise, free-living N-fixing diazotrophs have been associated with the rhizosphere of *T. latifolia* (Eckardt and Biesboer, 1988), which may enable cattails to

survive in low-N environments. The nitrogen-fixation rate peaked in August, when the cattail flowers were maturing and producing seed and when the stores of nitrogen in the rhizome were largely depleted. Therefore, the increased N-fixation rate coincided with the period when available-N in the environment was most beneficial to the cattails. The composition of denitrifying bacteria also differed between stands invaded by *T. x glauca* and nearby native plant stands has been found to differ (Angeloni et al., 2006). Whether there were functional differences between the two denitrifying bacteria population types was unknown. If the bacteria associated with cattails had a lower rate of denitrification than the bacteria associated with the native plant stand, then the process of nitrogen removal from the marsh system would be negatively impacted. In turn, eutrophication rates of the water would increase. Angeloni et al. (2006) found that sediments associated with *Typha* had a 14-fold increase in ammonium, a 10-fold increase in nitrate, and a 10-fold increase in phosphate compared to nearby native plant stands, which supported their theory that the cattails were reducing the ability of the marsh to remove nitrogen from the system. However, it is not clear from this study whether the increased nutrients were present before cattail colonization, or whether they increased after cattail expansion.

The importance of Olsen-P for the model may indicate that the pothole and ditch marshes of Manitoba were P-limited for hybrid cattail. I restricted the nutrient analysis to those available in the environment rather than measuring the levels in the plants and I am thus unable to conclude whether the marshes were N- or P-limited. All sites sampled were low in N, which ranged from 0 – 4.7 mg-NO₃ -N kg⁻¹ sediment. The sites ranged from low to medium fertility in terms of Olsen-P, which ranged from 0 to 38.8 mg-Olsen-P kg⁻¹

sediment. For comparison, Government of Manitoba (2007) recommends that fertilizer be applied to soils for growing corn when $\text{NO}_3 - \text{N}$ is under $25 \text{ mg-NO}_3 - \text{N kg}^{-1}$ soil and Olsen-P is considered to be at low levels when under $10 \text{ mg-Olsen-P kg}^{-1}$ soil. Therefore, it appears that some of the wetlands would not have been limited by P, but would more likely be limited by N. Further research, using the more accurate *in situ* resin-P methods would resolve the question of nutrient limitation in these wetlands.

Previous research has indicated that most marshes in North America are N-limited, but some are P-limited (Bedford et al, 1999; Craft et al., 2007). *T. x glauca* growth was enhanced by P fertilization in lacustrine marshes of the Great Lakes (Woo and Zedler, 2002; Boers and Zedler, 2008), whereas cattail growth was enhanced by N fertilization but not by P fertilization in Delta Marsh, a lacustrine marsh on the southern shore of Lake Manitoba (Neill, 1990). Thus, cattails can be either N-limited or P-limited, depending on local conditions. Understanding the local dynamics of N and P can help managers make informed decisions regarding wetland restoration and priorities. If a specific wetland was P-limited, then restricting N in the watershed would not help to restore the wetland, but reducing P may be beneficial, because reducing P in a P-limited marsh could reduce the growth of cattails.

Phosphorus and nitrogen bioavailability in wetland sediments vary as the redox potential changes with changes in sediment moisture throughout the season (Mitsch and Gosselink, 2000). These changes are particularly pronounced when sediment goes from anaerobic to aerobic or vice versa. Experiments on the effects of *T. domingensis* root oxygen stress and phosphorus uptake revealed that phosphorus uptake by the southern cattail was

dependent on the redox potential of the rhizosphere (DeLaune et al., 1999). Sampling methods such as the *in situ* resin method used by Nelson et al. (2007) more accurately reflect the bioavailability of nutrients such as P and N over time than the methods used in this study. In particular, during the process of air-drying, anaerobic sediment becomes aerobic and the forms of P and N can change as a result of the redox potential change. While the resin-P method is more accurate, it was not known to me at the time and so I performed the older methods that were routinely used. The benefit of these older methods is that they allow for direct comparisons with other studies that used the same methods.

Water pH was an important variable in the Full and FI models, where the *T. x glauca* proportion increased with increasing pH. Water pH is important to the availability of nutrients (Mitsch and Gosselink, 2000). The redox potential at which chemicals are stable in either reduced or oxidized states depends on the pH. The water pH of my sites ranged from neutral to alkaline (7.02 – 8.99). Under alkaline conditions, P becomes less available because it is bound by calcium and magnesium. When the pH is greater than 8, the availability of N may be reduced as under these alkaline conditions, the ammonium ion may be converted to NH₃, which is subsequently lost to the system through volatilization. Ammonia-N was the preferred N source for *T. latifolia* growth (Brix et al., 2002). Dyhr-Jensen and Brix (1996) demonstrated that while *T. latifolia* ammonia-N uptake was reduced at acidic pH levels less than five, the uptake of ammonia-N was constant over the pH range of 5-8. The effects of pH on nutrient uptake by other cattail species is unknown. If the different cattail species vary in their nutrient uptake efficiency under different environmental conditions and if such important differences exist within

the range of environments surveyed in this study, then these functional differences could be a source of missing data for the model formation.

Litter depth was also an important predictor variable in the FI model. The *T. x glauca* proportion increased with increasing litter depth. Litter depth and high biomass production have been linked to cattail invasiveness in Great Lakes lacustrine marshes (Freyman, 2008; Farrer and Goldberg, 2009; Vaccaro et al., 2009). Higher litter depths were expected in wetlands with greater proportions of hybrid cattail, because the hybrid cattail tends to be taller and grow more densely than *T. latifolia* (Travis et al., 2010) and thus would deposit more litter. Cattail litter excludes other plant species through shading without having any detrimental effects on its own growth when the litter layer was less than 50 cm (Jordan et al., 1990). In my study, the maximum litter depth was 14 cm, so the litter layer was not expected to be detrimental to cattail growth. Given the large number of wetlands in this study that had an average litter depth of zero but still had high proportions of the hybrid cattail, factors other than litter depth were likely more important in the hybrid cattail distribution in these wetlands.

Surrounding land use was also an important term in the Full and FI models. The proportion of *T. x glauca* was greatest when the surrounding land use was cropland and lower for pasture/hay land and bush. Nutrient run-off was expected to be greatest for marshes surrounded by crop land than for either pasture/hay or bush, as crops tend to be more heavily fertilized than pasture or hay land, and bush would not be fertilized by producers. Thus, nutrient levels within marshes next to crops were expected to be higher than marshes next to pasture/hay or bush. In the Great Lakes region, Vaccaro (2005)

linked increasing agricultural intensity with *T. x glauca* dominance. It is unclear why *T. x glauca* was associated with cropland and with lower Olsen-P. This highlights the need for further research into the nutrient dynamics of wetlands and the persistence of cattails, using more accurate resin P methods.

Sediment texture was not an important variable for *T. x glauca* distribution in this study. However, one survey study along the U.S. coast of the Great Lakes found that *Typha x glauca* was associated with organic soils, while *T. angustifolia* was associated with clay soils, and *T. latifolia* was not associated with either soil type (Johnston et al., 2007). The organic-C content in the sediment at my sites ranged from 1.4 to 18.3%, which is lower than the average loss-on-ignition organic-C content of 39.5% reported by Johnston et al. (2007). The method for determining texture in the study by Johnston et al. (2007) was by determining the proportion by weight of ashed soil that passed through a fine mesh sieve, which was different from the hydrometer method that I used. My study included only mixed stands of *T. x glauca* and *T. latifolia* and *T. x glauca* monocultures and omitted the one site where *T. angustifolia* was present. This omitted site had a sediment texture of 17% clay, and the sites that remained in the study ranged from 2-43% clay with a mean of 15%. My study only included pothole and ditch marshes, whereas the Johnston et al. (2007) study focused on lacustrine marshes of the Great Lakes. A study of habitat types of the cattail species and hybrid that covered a larger geographical range and encompassed all cattail habitat types would be required to verify whether sediment texture is generally important to the different cattail species or if it is only important in specific regions, or specific habitat types.

Water column conductivity did not contribute to decreasing the residual deviance of the model and its removal significantly improved the model. Therefore, conductivity was not associated with the distribution of hybrid cattail in Manitoba. Within the conductivity ranges of my study of 251-3247 $\mu\text{S cm}^{-1}$, there appears to be no difference in salinity tolerances of *T. latifolia* and *T. x glauca*. However, salinity tolerances of the cattail species and hybrid needs to be quantified experimentally. In Nebraska, *T. angustifolia* was more tolerant of high salinity than *T. latifolia*, with *T. x glauca* displaying intermediate tolerance (McMillan, 1959). However, *T. angustifolia* was so rare in my study of Manitoba cattail distribution that it was excluded from analysis. Soil solution is considered to be non-saline under 2000 $\mu\text{S cm}^{-1}$, and is slightly saline between 2000 - 4000 $\mu\text{S cm}^{-1}$ (Manitoba Agriculture, Food and Rural Development, 2014). Therefore, all of the sites in my study were non-saline to slightly saline and the cattails were not expected to be adversely affected by conductivity.

The lack of correlations between sampling date and the other environmental variables indicates that nutrient availability did not vary with sampling date overall. However, it is possible that nutrient availability had varied throughout the season in each wetland, especially if the marshes were ephemeral and lost their water by the end of the season. Because each wetland was only sampled once throughout the growing season, the within wetland variation across the season was unknown.

Geographic location within my area of study was not important to *T. x glauca* distribution as neither GPSEasting nor GPSNorthing were important variables in the final model, FI model. Sediment texture as percent clay decreased from east to west, and the

logarithm of sediment ammonium-N increased from east to west. Both the logarithm of water conductivity and the logarithm of water DOC decreased from south to north. These correlations were not important to the *T. x glauca* distribution, because none of these above-listed variables significantly decreased the residual deviance and were omitted from the Full and FI models.

The logarithm of transect length was correlated with the logarithm of water DOC, the logarithm of sediment total-N, sediment nitrate-N and sediment organic-C. Sediment organic-C was also correlated with both nitrate-N and total-N. I combined the pothole and ditch marsh data, and these two marsh types may have differed in transect length. The two-sample Hotelling T^2 test that I performed tested whether the suite of environmental variables were different between pothole and ditch sites. The results revealed that even if there were differences between individual variables, those differences were small enough that the environments of potholes and ditches were equivalent.

Chance dispersal could be a missing variable. It is unknown whether dispersal limits cattail occurrence. Cattail seeds are wind-dispersed and numerous, with *T. latifolia* producing an average of 222,000 seeds per plant (Yeo, 1964). Resultant *T. x glauca* specimens from experimental crosses between *T. latifolia* and *T. angustifolia* produced 0-25% viable seed (Smith, 1967). Because the hybrid is mostly sterile (Marsh 1962; Smith, 1967), researchers have assumed that *T. x glauca* predominately spreads vegetatively. However if hybrid cattails produce up to 55,500 viable seeds, which is 25% of 222,000, then seed dispersal cannot be dismissed without evidence. Cattails spread vegetatively

through clonal expansion via rhizome growth, and through rhizome pieces being dispersed by water and animals (Smith, 1967). Vegetative growth can be rapid. In a greenhouse study, one seedling was observed to spread clonally to a diameter of 3 m and produce 34 mature aerial shoots within one growing season (Yeo, 1964), and *T. x glauca* has been observed spreading clonally in the Great Lakes area at 5.2 m per year (Smith, 1967). The surface water connections between marshes and ditches, including the short-term connections formed during spring melt and flooding events, are also likely important for cattail dispersal. Because cattails have multiple means of dispersal, produce such numerous seeds, and display rapid vegetative growth, dispersal may not be limiting to cattail distribution. However, this needs to be verified experimentally.

Given that *T. latifolia*, *T. angustifolia*, (Grace and Wetzel, 1981) and *T. x glauca* (Waters and Shay, 1992) have different water depth tolerances, basin morphometry may be another missing variable from the distribution model.

The presence of cattail does not necessarily mean that it is invasive at that location and that all other vegetation will be displaced through time. Bevington (2007) found no difference in biodiversity between *Typha*-dominated stands and stands that were not dominated by cattails in created wetlands that were at least 15 years old in Virginia. The marshes in my study included the extremes of homogenous cattail monocultures and clumps of cattail interspersed within a heterogenous mixture of emergent species, as well as intermediates between these extremes. With no knowledge of the age of the wetlands or of cattail colonization date, I cannot determine whether or not the cattails are

expanding within the marshes or not. Wetland age and date of colonization could be important missing variables in the model.

For the purposes of this study, I assumed that all of *T. x glauca* were of similar genetic origin and therefore should respond to the same environmental variables similarly across the study area. Most of the hybrid cattail in North America that have been genetically analyzed were F₁ hybrids between *T. latifolia* and *T. angustifolia* (Marcinko-Kuehn and White, 1999; Travis et al., 2010; Kirk et al., 2011). Experimental crosses indicate that introgression would be unlikely in nature because the F₁ hybrids were mostly sterile. By comparing the viability of different experimental crosses between *T. latifolia* and *T. angustifolia*, one study concluded that the pollen source must be from *T. latifolia* (Smith, 1967), but another concluded that the pollen source would more likely be *T. angustifolia* (Marsh, 1962). To date, the majority of backcrossing has been with *T. angustifolia*, because most hybrid specimens that were not of the F₁ generation were more genetically similar to *T. angustifolia* than *T. latifolia* (Lee, 1975; Mashburn et al., 1978; Sharitz et al., 1980; Travis et al., 2010; Kirk et al., 2011). However, Kirk et al. (2011), also found a few introgressed individuals that were more genetically similar to *T. latifolia*. If the *T. x glauca* in Manitoba were mixes of F₁ and introgressed hybrids, then treating them as homogenous would account for some of the error in the final model. Because introgressed hybrids are rare, introgression with *T. latifolia* is especially rare in eastern North America, and *T. angustifolia* is very rare in Manitoba, my assumption that the hybrid cattail in this study are of the F₁ generation is reasonable, but cannot be validated without genetic analysis.

The leaf-lamina-margin identification method was chosen, because it was more accurate than using gross external morphology, and because genetic analysis was unavailable. The method has the advantage that it relies on characters within vegetative tissue, which expands the available sampling window to when leaves are mature to their senescence, rather than limiting it to when the plants are in flower. The method also allowed for less biased sampling because even marshes that did not have cattails in flower could be sampled, rather than being limited to those specimens in flower. While it does have a number of advantages, the leaf-lamina-margin method has only been used by one previous study, in one location (McManus et al., 2002). In that study, however, the leaf-lamina-margin method was validated by genetic analysis. The frequency distributions of leaf width (Fig. 3.13) and logarithm of leaf length/leaf width (Fig. 3.14) of 416 cattail ramets collected in southwestern Manitoba and southeastern Saskatchewan in 2009 and 2011 as identified with leaf-lamina-margin method also support this method. Out of the 416 cattail ramets, 331 specimens were *T. x glauca*, 80 were *T. latifolia*, and 5 were *T. angustifolia*. The frequency distributions for both leaf widths and logarithm leaf length/leaf width of *T. latifolia* and *T. angustifolia* overlap, but their peaks are separate. The frequency distributions of leaf width for *T. x glauca* overlaps both *T. latifolia* and *T. angustifolia*, as expected. The frequency distributions of logarithm leaf length/leaf width for *T. x glauca* overlaps both *T. latifolia* and *T. angustifolia*. The frequency distribution of *T. angustifolia* logarithm leaf length/leaf width has two peaks, where one peak coincides with the peak for *T. x glauca*. This unexpected peak for *T. angustifolia* is the result of just one sample at Delta Marsh in 2009. This specimen may be either a

misidentified *T. x glauca* specimen, or it may be a correctly identified *T. angustifolia* specimen with a logarithm leaf length/leaf width comparable to *T. x glauca*. Genetic analysis is required to resolve this issue. The leaf-lamina-margin method has great potential for accurate cattail identification where genetic analysis is not available, but it does need further validation through genetic analysis of cattails in different regions.

Understanding how cattails respond to different environments requires a combination of long-term surveys and experimental studies, combined with accurate species and hybrid identification, preferably through genetic analysis. The interplay between cattail genetics and environmental conditions on cattail growth and dispersal may vary depending on marsh type. Because local environmental conditions vary by wetland type, hydrology, nutrient relations, and soil type, survey studies should encompass broad areas to sample as many of the habitats as possible. In particular, studies within lacustrine, riverine, and pothole marsh types are necessary, because their differences in hydrology may modify how cattails respond to environmental variables. While it is often assumed that the hybrid is the most invasive cattail, both of the parent species can also be invasive, and the differences in invasive tendencies are poorly understood for *T. latifolia*, *T. angustifolia*, and *T. x glauca*. Evaluation of invasiveness is further complicated by the fact that what is known as *T. x glauca* includes the F₁ and F₂ generations, as well as introgressed hybrids. Understanding to what degrees cattail genetics and the environmental conditions are linked to invasiveness would be of great benefit to wetland managers attempting to restore wetlands or to prevent cattail dominance, because it would enable them to focus their resources more effectively. Would it be more beneficial to focus resources into

eliminating one species of cattail in favour of another, or, if all cattails have the same invasive tendencies, what environmental factors are most important for reducing the chances of cattail dominance? These questions need to be thoroughly investigated so that wetland managers can utilize their resources effectively to restore wetlands and to prevent further encroachment by cattail.

Table 3.1 Cattail leaf-lamina-margin characters for discrimination between *Typha latifolia*, *T. angustifolia*, and *T. x glauca*, adapted from McManus et al. (2002)

	<i>T. latifolia</i>	<i>T. angustifolia</i>	<i>T. x glauca</i>
Shape of leaf edge (oblong / wedge)	Oblong	Wedge	Wedge
Number of vascular bundles within zone of fibres at leaf edge	1	1 – 4	1 – 2
Enlargement and thickening of epidermal cells above vascular bundles	Present	Absent	Present
Arrangement of mesophyll cells (Loose arch / I-beam)	Loose arch	Loose arch to I-beam	I-beam

Table 3.2 Percentages of *Typha x glauca* and *T. latifolia* counted at pothole and ditch marshes sampled in southwestern Manitoba and southeastern Saskatchewan, 2011. See Appendix A for GPS coordinates

Pothole Site #	<i>T. x glauca</i> (%)	<i>T. latifolia</i> (%)	Ditch Site #	<i>T. x glauca</i> (%)	<i>T. latifolia</i> (%)
14	100	0	201	100	0
15	17	83	202	100	0
16	67	33	203	50	50
17	0	100	204	33	67
18	83	17	205	100	0
20	100	0	206	83	17
23	0	100	208	100	0
24	100	0	210	100	0
25	100	0	212	83	17
27	67	33	213	100	0
28	100	0	214	17	83
30	100	0	215	33	67
33	83	17	220	100	0
34	67	33	221	100	0
35	83	17	224	100	0
36	83	17	226	50	50
37	100	0			
38	33	67			
40	100	0			
41	50	50			
42	100	0			
43	83	17			
48	83	17			

Table 3.3 Sediment and water column environmental variables plus transect length and average litter depth and their range, mean, standard deviation (SD), and percent coefficient of variation (CV) in ditch and pothole marshes in southwestern Manitoba and southeastern Saskatchewan, 2011. The average standard deviation of replicate samples is shown in brackets beside the environmental variable name, where applicable

Variable			CV		
Type	Environmental Variable	Range	Mean	SD	%
Sediment	Texture (% Clay)	2 – 43	15	10	67.8
	Organic C (g-organic-C kg ⁻¹)	14.0 – 182.9	52.2	32.1	61.4
	Total-N (g-N kg ⁻¹) (\pm 0.16)	1.2 – 16.4	4.8	2.9	60.6
	Ammonium-N (mg-NH ₄ -N kg ⁻¹) (\pm 9.1)	2.0 – 42.9	12.0	8.8	73.6
	Nitrate-N (mg-NO ₃ -N kg ⁻¹) (\pm 1.7)	0.0 – 4.7	1.4	1.4	101.6
	OlsenP (mg-Olsen-P kg ⁻¹) (\pm 0.2)	0.0 – 38.8	10.7	8.5	79.6
Water Column	Conductivity (μ S cm ⁻¹)	251 – 3247	1023	699	68.3
	pH	7.02 – 8.99	8.11	0.54	6.7
	Dissolved-N (mg-N L ⁻¹) (\pm 0.8)	1.7 – 99.9	7.8	15.4	197.2
	DOC (mg-DOC L ⁻¹) (\pm 0.6)	37.5 – 252.9	82.6	36.6	44.3
Other	Transect Length (m)	2 – 50	11	8	74.0
	Average Litter Depth (cm) (\pm 3.0)	0 – 14	3	4	127.4

Table 3.4 ANOVA linear regression of all combinations of the following variables from 2011 pothole and ditch marshes in Manitoba and eastern Saskatchewan: date, GPS easting, GPS northing, Ln of transect length, litter depth, Ln of water conductivity, water pH, Ln of water dissolved-N, Ln of water DOC, sediment texture, Olsen-P, Ln of total-N, Ln of ammonium-N, nitrate-N, and organic-C; d.f. = 1, 37, n=39. The r^2 for statistically significant results were shown. Continued on the following two pages

X variable	Y variable	F	P	r^2
Date	GPSEasting	0.13	0.910	---
Date	GPSNorthing	1.67	0.204	---
Date	LengthLn	0.21	0.649	---
Date	Litter	1.30	0.262	---
Date	ConductivityLn	0.15	0.696	---
Date	pH	0.49	0.489	---
Date	DNLn	0.69	0.412	---
Date	DOCLn	0.10	0.749	---
Date	Texture	0.79	0.381	---
Date	OlsenP	1.24	0.273	---
Date	TotalNLn	0.00	0.979	---
Date	AmmoniumLn	0.00	0.990	---
Date	Nitrate	0.09	0.763	---
Date	OrganicC	0.01	0.904	---
GPSEasting	GPSNorthing	2.52	0.121	---
GPSEasting	LengthLn	1.11	0.299	---
GPSEasting	Litter	1.58	0.216	---
GPSEasting	ConductivityLn	0.14	0.710	---
GPSEasting	pH	0.05	0.825	---
GPSEasting	DNLn	0.11	0.746	---
GPSEasting	DOCLn	0.38	0.540	---
GPSEasting	Texture	5.32	0.027	0.126
GPSEasting	OlsenP	1.44	0.238	---
GPSEasting	TotalNLn	1.55	0.222	---
GPSEasting	AmmoniumLn	9.32	0.004	0.201
GPSEasting	Nitrate	0.17	0.684	---
GPSEasting	OrganicC	1.17	0.286	---
GPSNorthing	LengthLn	0.44	0.509	---
GPSNorthing	Litter	1.29	0.264	---
GPSNorthing	ConductivityLn	11.08	0.002	0.231
GPSNorthing	pH	0.70	0.408	---
GPSNorthing	DNLn	0.35	0.561	---

Table 3.4 (Continued)

X variable	Y variable	F	P	r^2
GPSNorthing	DOCLn	6.01	0.019	0.140
GPSNorthing	Texture	1.92	0.174	---
GPSNorthing	OlsenP	0.57	0.454	---
GPSNorthing	TotalNLn	0.20	0.656	---
GPSNorthing	AmmoniumLn	0.23	0.633	---
GPSNorthing	Nitrate	0.68	0.414	---
GPSNorthing	OrganicC	0.19	0.666	---
LengthLn	Litter	0.33	0.567	---
LengthLn	ConductivityLn	0.22	0.642	---
LengthLn	pH	0.51	0.480	---
LengthLn	DNLn	3.32	0.076	---
LengthLn	DOCLn	5.29	0.027	0.125
LengthLn	Texture	1.62	0.211	---
LengthLn	OlsenP	0.08	0.776	---
LengthLn	TotalNLn	5.94	0.020	0.138
LengthLn	AmmoniumLn	1.78	0.190	---
LengthLn	Nitrate	4.19	0.048	0.102
LengthLn	OrganicC	7.12	0.011	0.161
Litter	ConductivityLn	0.58	0.453	---
Litter	pH	0.04	0.838	---
Litter	DNLn	0.02	0.896	---
Litter	DOCLn	0.28	0.598	---
Litter	Texture	0.01	0.938	---
Litter	OlsenP	0.00	0.959	---
Litter	TotalNLn	1.02	0.318	---
Litter	AmmoniumLn	0.55	0.465	---
Litter	Nitrate	1.67	0.204	---
Litter	OrganicC	1.22	0.276	---
ConductivityLn	pH	0.31	0.579	---
ConductivityLn	DNLn	4.87	0.034	0.116
ConductivityLn	DOCLn	16.25	2.66E-04	0.305
ConductivityLn	Texture	2.18	0.148	---
ConductivityLn	OlsenP	0.08	0.779	---
ConductivityLn	TotalNLn	0.44	0.509	---
ConductivityLn	AmmoniumLn	1.92	0.174	---
ConductivityLn	Nitrate	0.13	0.716	---
ConductivityLn	OrganicC	0.25	0.619	---

Table 3.4 (Continued)

X variable	Y variable	F	P	r^2
pH	DNLn	1.66	0.205	---
pH	DOCLn	0.11	0.740	---
pH	Texture	0.08	0.783	---
pH	OlsenP	1.07	0.307	---
pH	TotalNLn	1.51	0.227	---
pH	AmmoniumLn	0.95	0.336	---
pH	Nitrate	0.69	0.411	---
pH	OrganicC	2.80	0.103	---
DNLn	DOCLn	53.80	1.02E-08	0.593
DNLn	Texture	0.03	0.869	---
DNLn	OlsenP	0.16	0.693	---
DNLn	TotalNLn	0.26	0.612	---
DNLn	AmmoniumLn	1.81	0.187	---
DNLn	Nitrate	0.05	0.823	---
DNLn	OrganicC	0.41	0.527	---
DOCLn	Texture	0.71	0.404	---
DOCLn	OlsenP	0.00	0.967	---
DOCLn	TotalNLn	0.02	0.886	---
DOCLn	AmmoniumLn	1.19	0.282	---
DOCLn	Nitrate	0.05	0.817	---
DOCLn	OrganicC	0.55	0.463	---
Texture	OlsenP	3.13	0.085	---
Texture	TotalNLn	2.58	0.117	---
Texture	AmmoniumLn	7.17	0.011	0.162
Texture	Nitrate	0.11	0.743	---
Texture	OrganicC	3.36	0.075	---
OlsenP	TotalNLn	5.55	0.024	0.130
OlsenP	AmmoniumLn	1.97	0.169	---
OlsenP	Nitrate	0.54	0.469	---
OlsenP	OrganicC	2.03	0.163	---
TotalNLn	AmmoniumLn	11.53	0.002	0.238
TotalNLn	Nitrate	1.59	0.215	---
TotalNLn	OrganicC	58.52	3.93E-09	0.613
AmmoniumLn	Nitrate	1.49	0.230	---
AmmoniumLn	OrganicC	10.41	0.003	0.220
Nitrate	OrganicC	5.05	0.031	0.120

Table 3.5 Analysis of deviance of quasi-binomial GLM of *Typha x glauca* proportion models with each possible single predictor variable against the null model. Data was from pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011, n=39. Percent explained deviance was calculated for models that were significantly different from the null model (P=0.05)

Model	d.f.	Δ Deviance	Residual Deviance	F	P	Explained deviance (%)
Null	38	---	134.98	---	---	---
~ $\beta_0 + \beta\text{Date}$	37	0.07	134.90	0.02	0.883	---
~ $\beta_0 + \beta\text{GPS}Easting$	37	0.79	134.19	0.24	0.624	---
~ $\beta_0 + \beta\text{GPS}Northing$	37	2.70	132.28	0.86	0.359	---
~ $\beta_0 + \beta\text{ConductivityLn}$	37	0.09	134.89	0.03	0.869	---
~ $\beta_0 + \beta\text{pH}$	37	8.50	126.47	2.74	0.107	---
~ $\beta_0 + \beta\text{DNLn}$	37	4.07	130.90	1.25	0.272	---
~ $\beta_0 + \beta\text{DOCLn}$	37	1.60	133.38	0.48	0.492	---
~ $\beta_0 + \beta\text{Texture}$	37	0.92	134.06	0.28	0.599	---
~ $\beta_0 + \beta\text{OlsenP}$	37	20.38	114.59	7.45	0.010	15.1
~ $\beta_0 + \beta\text{TotalNLn}$	37	0.55	134.42	0.17	0.684	---
~ $\beta_0 + \beta\text{AmmoniumLn}$	37	0.10	134.88	0.03	0.865	---
~ $\beta_0 + \beta\text{Nitrate}$	37	1.24	133.74	0.38	0.540	---
~ $\beta_0 + \beta\text{OrganicC}$	37	0.40	134.58	0.12	0.729	---
~ $\beta_0 + \beta\text{Litter}$	37	9.87	125.10	3.36	0.075	---
~ $\beta_0 + \beta\text{LengthLn}$	37	0.84	134.14	0.25	0.617	---
~ $\beta_0 + \beta\text{LandUse}$	36	0.27	134.70	0.04	0.960	---

Table 3.6 Analysis of deviance of P1, potential full quasi-binomial GLM of *Typha x glauca* distribution in pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011. Where, $P1 \sim \beta_0 + \beta_1\text{Texture} + \beta_2\text{Ammonium-NLn} + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_5\text{DOCLn} + \beta_6\text{pH} + \beta_7\text{Date} + \beta_8\text{Litter} + \beta_9\text{LandUse}$. Terms added sequentially from first to last

Variable added	Δ d.f.	Δ Deviance	Residual d.f.	Residual Deviance
Null	---	---	38	134.98
Texture	1	0.92	37	134.06
AmmoniumLn	1	0.60	36	133.47
Nitrate	1	4.14	35	129.32
OlsenP	1	17.69	34	111.63
DOCLn	1	0.57	33	111.06
pH	1	3.55	32	107.50
Date	1	2.47	31	105.03
Litter depth	1	9.98	30	95.05
Land Use	3	2.61	28	92.44

Table 3.7 Analysis of deviance of P2, potential full quasi-binomial GLM of *Typha x glauca* distribution in pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011. Where, $P2 \sim \beta_0 + \beta_1\text{Texture} + \beta_2\text{Ammonium-NLn} + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_7\text{Date} + \beta_8\text{Litter} + \beta_9\text{LandUse}$. Terms added sequentially from first to last

Variable added	Δ d.f.	Δ Deviance	Residual d.f.	Residual Deviance
Null	---	---	38	134.98
Texture	1	0.92	37	134.06
AmmoniumLn	1	0.60	36	133.47
Nitrate	1	4.14	35	129.32
OlsenP	1	17.69	34	111.63
pH	1	3.69	33	107.94
Date	1	2.66	32	105.29
Litter depth	1	9.84	31	95.45
Land Use	2	2.01	29	93.44

Table 3.8 Analysis of deviance of P3, potential full quasi-binomial GLM of *Typha x glauca* distribution in pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011. Where, $P3 \sim \beta_0 + \beta_1\text{Texture} + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_7\text{Date} + \beta_8\text{Litter} + \beta_9\text{LandUse}$. Terms added sequentially from first to last

Variable added	Δ d.f.	Δ Deviance	Residual d.f.	Residual Deviance
Null	---	---	38	134.98
Texture	1	0.92	37	134.06
Nitrate	1	3.44	36	130.62
OlsenP	1	18.46	35	112.16
pH	1	3.99	34	108.17
Date	1	2.32	33	105.85
Litter depth	1	8.62	32	97.23
Land Use	2	1.79	30	95.44

Table 3.9 Analysis of deviance of P4, potential full quasi-binomial GLM of *Typha x glauca* distribution in pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011. Where, $P4 \sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_7\text{Date} + \beta_8\text{Litter} + \beta_9\text{LandUse}$. Terms added sequentially from first to last

Variable added	Δ d.f.	Δ Deviance	Residual d.f.	Residual Deviance
Null	---	---	38	134.98
Nitrate	1	3.65	37	131.32
OlsenP	1	18.73	36	112.59
pH	1	4.08	35	108.51
Date	1	2.01	34	106.50
Litter depth	1	8.60	33	97.90
Land Use	2	1.72	31	96.19

Table 3.10 Analysis of deviance of P5, potential full quasi-binomial GLM of *Typha x glauca* distribution in pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011. Where, $P5 \sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse}$. Terms added sequentially from first to last

Variable added	Δ d.f.	Δ Deviance	Residual d.f.	Residual Deviance
Null	---	---	38	134.98
Nitrate	1	3.65	37	131.32
OlsenP	1	18.73	36	112.59
pH	1	4.08	35	108.51
Litter depth	1	9.47	34	99.04
Land Use	2	2.76	32	96.28

Table 3.11 Quasi-binomial GLM analysis of deviance of both the Full model and the FI model each versus the Null model. Where Full model $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse}$, and FI model $\sim \beta_0 + \beta_3\text{Nitrate} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_3\text{Nitrate} : \beta_4\text{OlsenP}$. Models of *Typha x glauca* distribution in pothole and ditch marshes southwestern Manitoba and southeastern Saskatchewan, 2011. Deviance explained was calculated with the following formula: $100 * (\text{Null deviance} - \text{Residual deviance}) / \text{Null deviance}$

Model	Residual d.f.	Residual Deviance	Δ d.f.	Δ Deviance	F	P	Explained deviance (%)
Null	38	134.98	---	---	---	---	---
Full	33	96.56	5	38.42	2.73	0.036	28.5
FI	31	84.82	7	50.15	2.45	0.040	59.1

Table 3.12 Quasi-binomial GLM model comparison of nested candidate models to the Full model for *Typha x glauca* distribution in prairie pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011, at the P=0.05 significance level. The null model was shown for reference. Deviance explained was calculated only for models that were different from the Full model with the following formula: $100 * (\text{Null deviance} - \text{Residual deviance}) / \text{Null deviance}$

Model and description	d.f.	Residual Deviance	F	P	Explained deviance (%)
Null $\sim \beta_0$	38	134.98	---	---	---
Full $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse}$	33	96.56	---	---	28.5
M1 $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH}$	36	109.91	1.58	0.212	---
M2 $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter}$	35	99.71	0.56	0.577	---
M3 $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_9\text{LandUse}$	34	104.65	2.88	0.991	---
M4 $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_8\text{Litter}$	36	104.39	0.93	0.438	---
M5 $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_8\text{Litter} + \beta_9\text{LandUse}$	34	101.58	1.79	0.191	---
M6 $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_9\text{LandUse}$	35	109.75	2.35	0.112	---
M7 $\sim \beta_0 + \beta_6\text{pH} + \beta_8\text{Litter}$	36	115.19	2.22	0.105	---
M8 $\sim \beta_0 + \beta_6\text{pH} + \beta_9\text{LandUse}$	35	125.91	5.22	0.011	6.7
M9 $\sim \beta_0 + \beta_8\text{Litter} + \beta_9\text{LandUse}$	35	124.63	5.00	0.013	7.7

Table 3.13 Quasi-binomial GLM model comparison of the Full model with candidate models that are the Full model plus one term that had been previously dropped, at the P=0.05 significance level. Models of *Typha x glauca* distribution in prairie pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011. The null model was shown for reference

Model and description		Residual			
		d.f.	Deviance	F	P
Null	$\sim \beta_0$	38	134.98	---	---
Full	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse}$	33	96.56	---	---
M10	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_{10}\text{GPSEasting}$	32	95.68	0.31	0.585
M11	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_{11}\text{GPSNorthing}$	32	94.10	0.91	0.347
M12	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_{12}\text{ConductivityLn}$	32	96.31	0.09	0.769
M13	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_{13}\text{LengthLn}$	32	95.31	0.44	0.511
M14	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_{14}\text{OrganicC}$	32	94.71	0.69	0.413
M15	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_{15}\text{DNLn}$	32	94.76	0.63	0.433
M16	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_2\text{AmmoniumLn}$	32	95.54	0.37	0.548
M17	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_1\text{Texture}$	32	95.97	0.19	0.664
M18	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_3\text{Nitrate}$	32	96.28	0.09	0.761
M19	$\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_7\text{Date}$	32	96.48	0.03	0.865

Table 3.14 Quasi-binomial GLM model comparison of nested candidate models to the FI model for *Typha x glauca* distribution in prairie pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011, at the P=0.05 significance level. The null model was shown for reference

Model and description		d.f.	Residual Deviance	F	P
Null	$\sim \beta_0$	38	134.98	---	---
FI	$\sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_3\text{Nitrate-N} : \beta_4\text{OlsenP}$	31	84.82	---	---
M21	$\sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_3\text{Nitrate-N} : \beta_4\text{OlsenP}$	34	100.29	1.76	0.175
M22	$\sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_3\text{Nitrate-N} : \beta_4\text{OlsenP}$	33	87.59	0.47	0.628
M23	$\sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_9\text{LandUse} + \beta_3\text{Nitrate-N} : \beta_4\text{OlsenP}$	32	95.36	3.60	0.067
M24	$\sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_8\text{Litter} + \beta_3\text{Nitrate-N} : \beta_4\text{OlsenP}$	34	92.80	0.91	0.448
M25	$\sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_3\text{Nitrate-N} : \beta_4\text{OlsenP}$	32	90.49	1.94	0.174
M26	$\sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_9\text{LandUse} + \beta_3\text{Nitrate-N} : \beta_4\text{OlsenP}$	33	100.26	2.64	0.088
M27	$\sim \beta_0 + \beta_3\text{Nitrate-N} + \beta_4\text{OlsenP} + \beta_3\text{Nitrate-N} : \beta_4\text{OlsenP}$	35	104.67	1.69	0.176

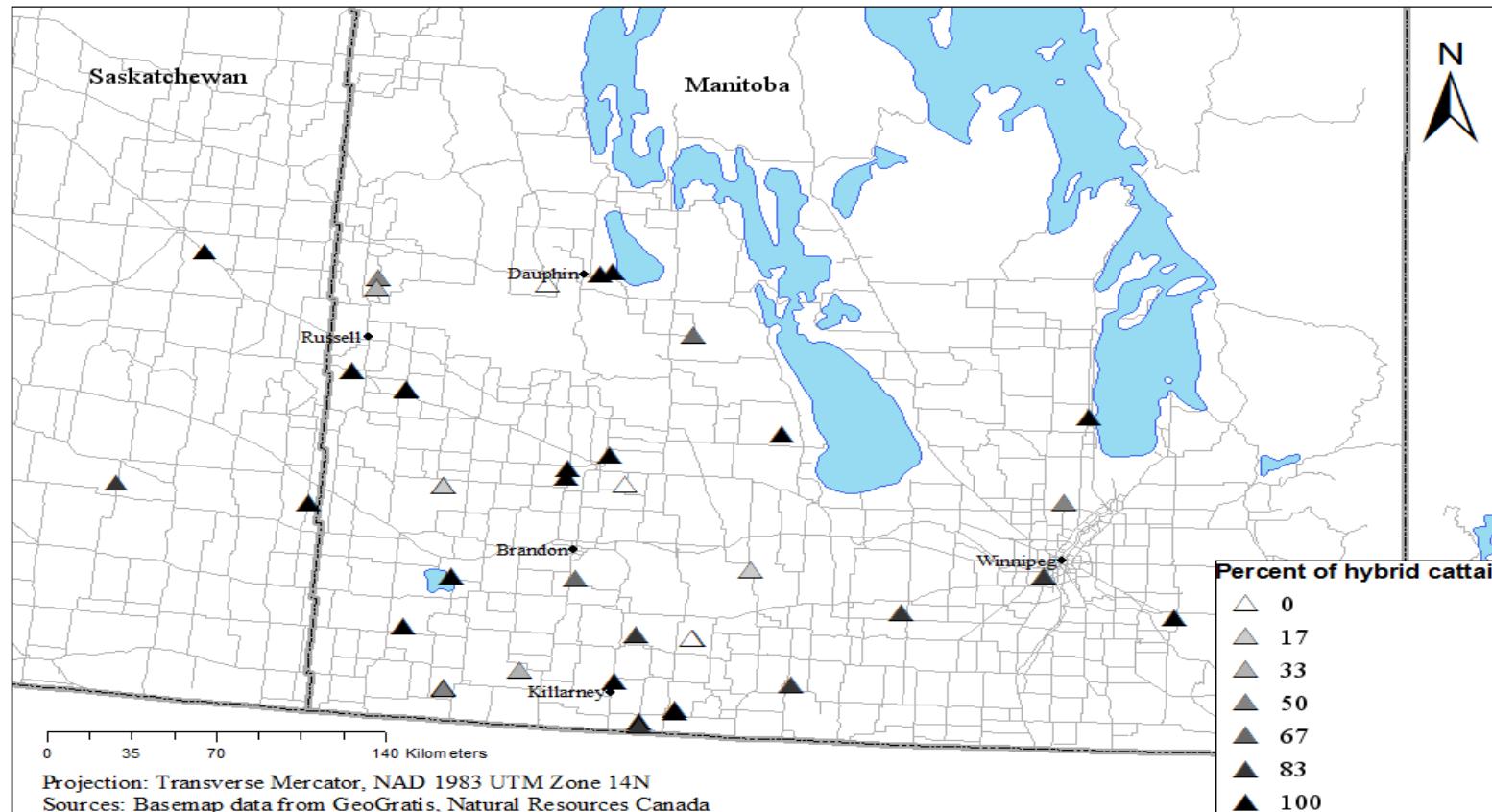


Fig. 3.1 Map of the percentage of *Typha x glauca* present at each prairie pothole or ditch study site in southwestern Manitoba and southeastern Saskatchewan, 2011. For the GPS coordinates of all transects, see Appendix A

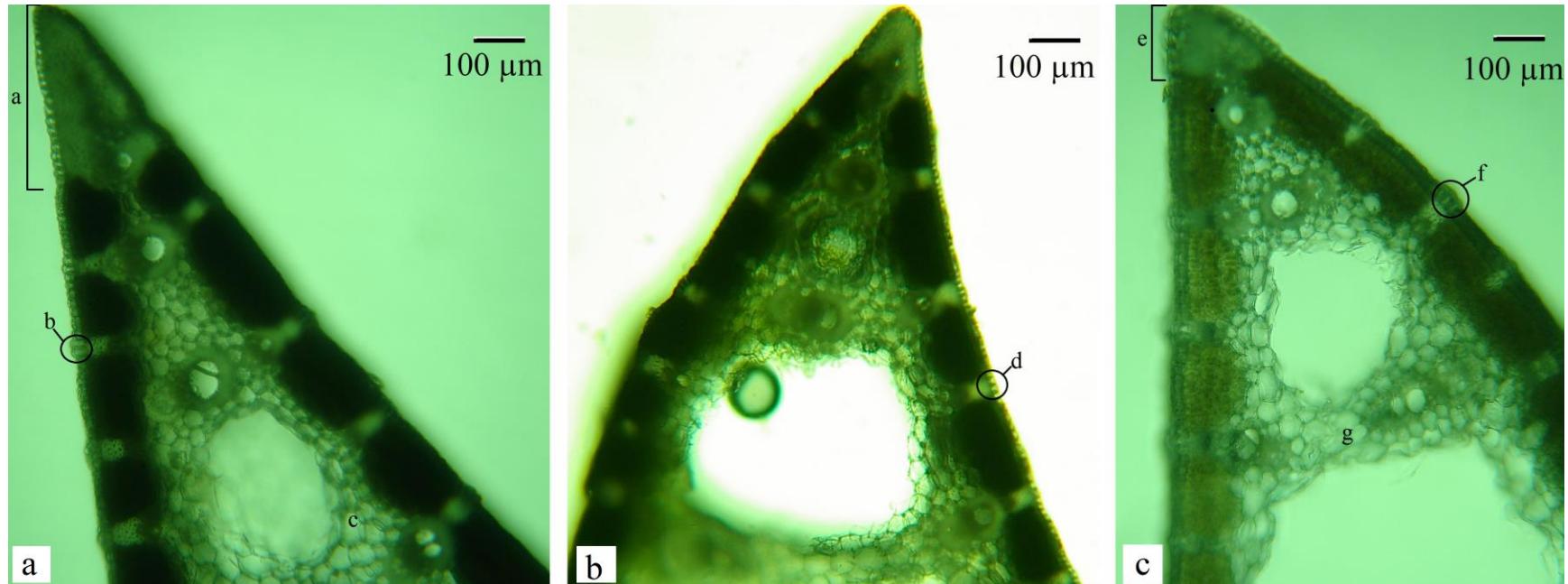


Fig. 3.2 Cattail leaf edge cross-sections viewed through a green filter. **a** *Typha latifolia*. Note the (a) oblong-shaped tip, (b) enlarged epidermal cells above the vascular bundles, and (c) more irregular arrangement of mesophyll cells. **b** *T. angustifolia*. Note the (d) absence of enlarged epidermal cells above vascular bundles. **c** *T. x glauca*. Note the (e) wedge-shaped tip, (f) enlarged epidermal cells above the vascular bundles, and the (g) I-beam arrangement of mesophyll cells



Fig. 3.3 Soil corer used to extract 10 cm long sediment cores from cattail pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011

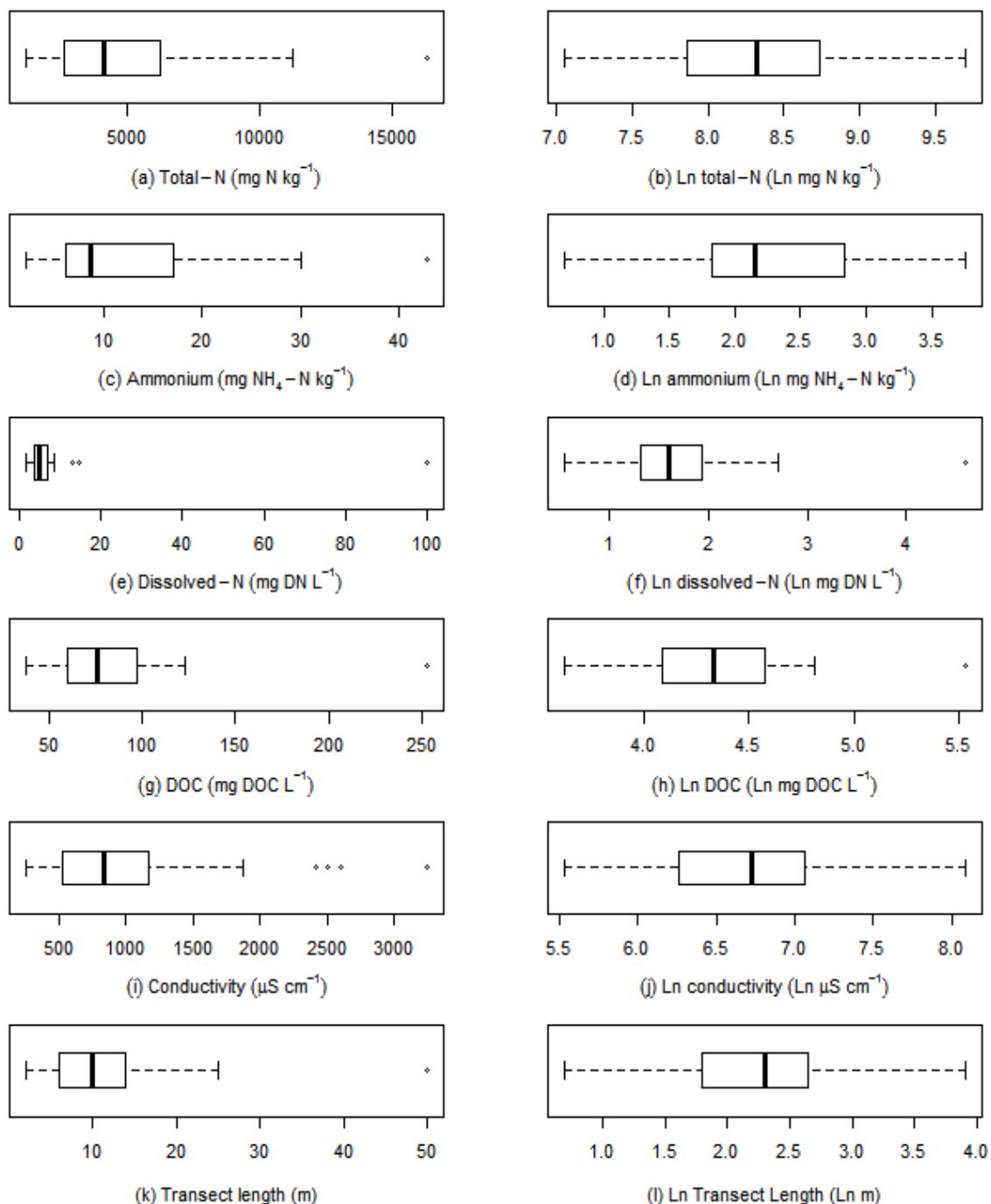


Fig. 3.4 Boxplots of original variables sediment total-N, and ammonium, water DN, DOC, and conductivity, and transect length (a, c, e, g, i, and k), and their transformed counterparts(b, d, f, h, j and l). From marshes in southwestern Manitoba and southeastern Saskatchewan, 2011. The boxes represent the range of values within the 25-75% percentiles, the ditto lines within the boxes are the median values, and the whiskers extend from the boxes to the minimum and maximum values. Points outside of the whiskers are potential outliers

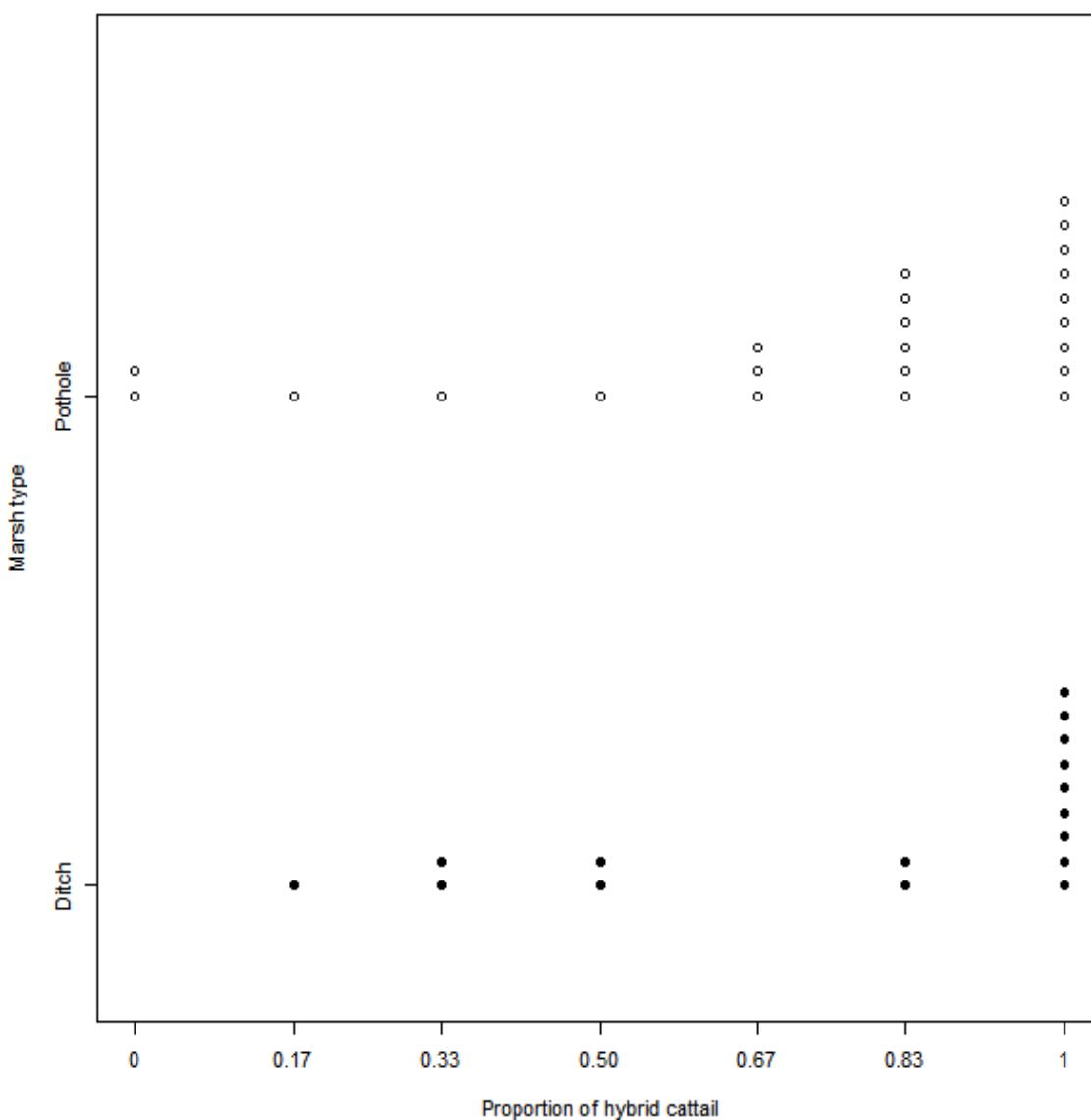


Fig. 3.5 Frequency distribution plot of the proportion of cattails identified as the hybrid, *Typha x glauca*, along each transect surveyed in ditch and prairie pothole marshes in southeastern Manitoba and southeastern Saskatchewan, 2011

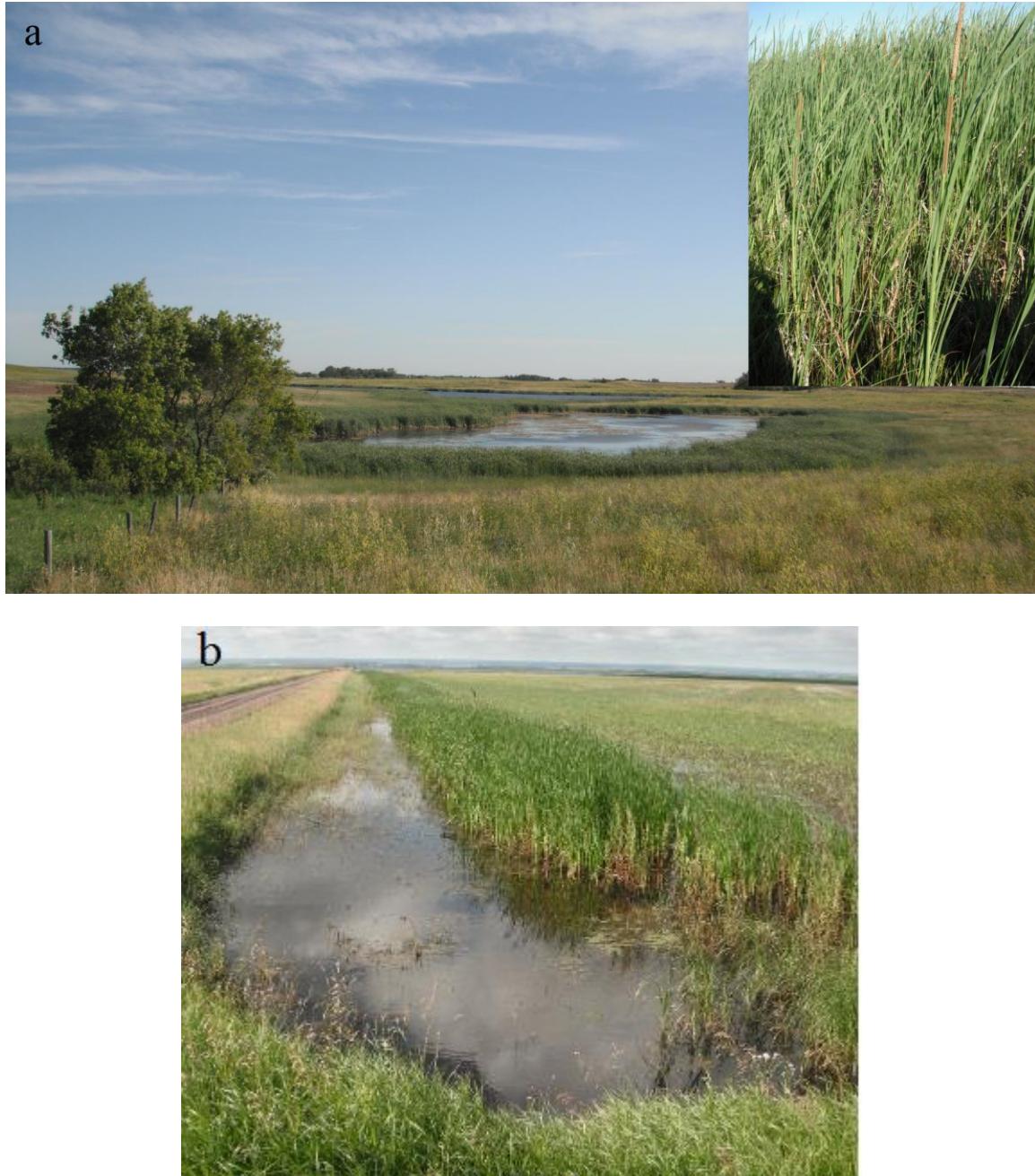


Fig. 3.6 Prairie pothole and ditch examples from Manitoba 2011 that demonstrate dense cattail monocultures. **a** Prairie pothole site #28 near Cartwright, MB, 2011. Inset picture at top right is a closer look at the sampled transect. Note the dense monoculture ring of *Typha x glauca* surrounding the open water. The transect was 100% *T. x glauca*. **b** Ditch site #203 near Boissevain, MB, 2011. The transect was 50% *T. x glauca* and 50% *T. latifolia*.

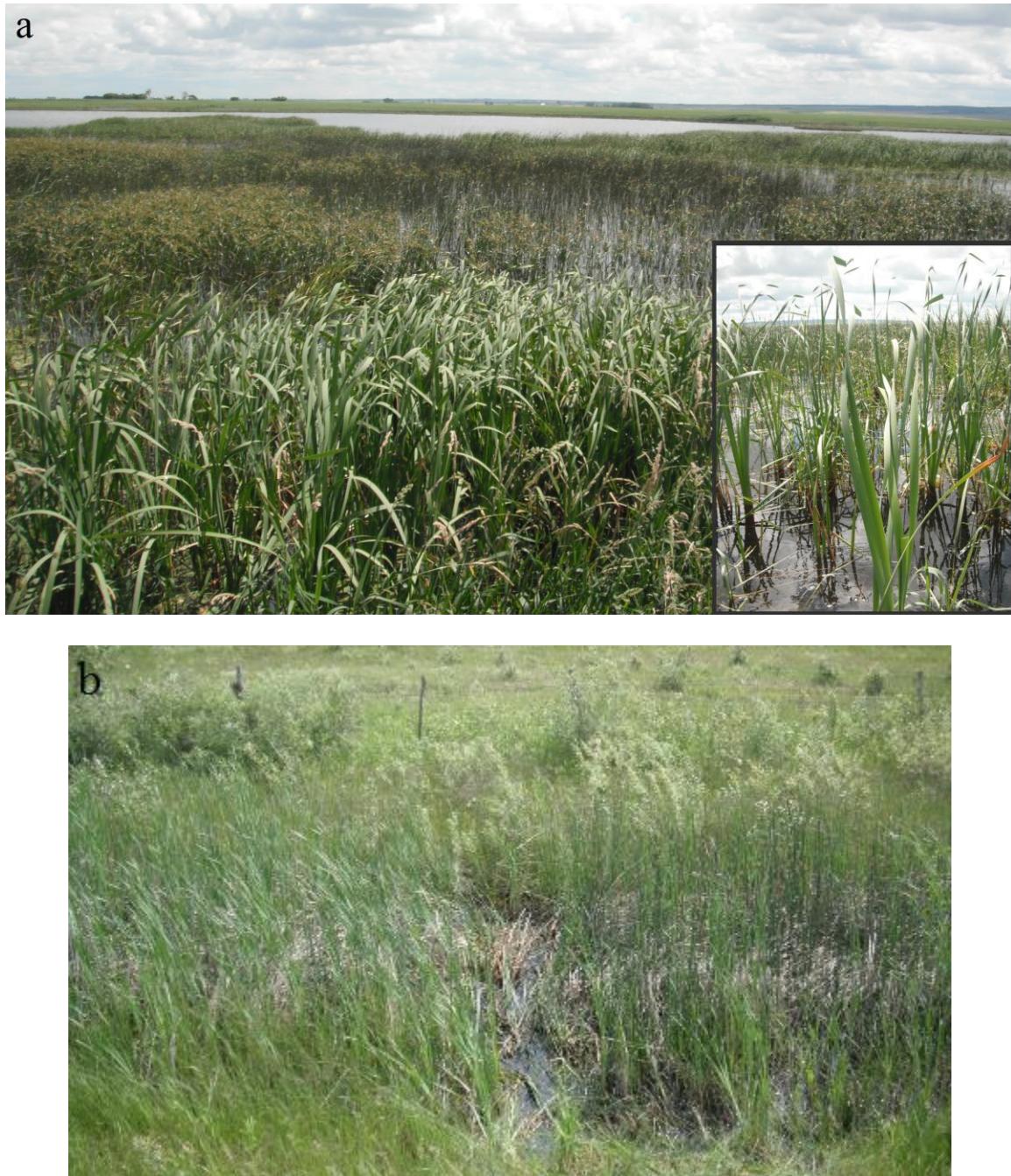


Fig. 3.7 Prairie pothole and ditch examples that demonstrate heterogenous structure of cattails and other emergent species. **a** Prairie pothole site #36 near Deloraine, MB. Inset picture at bottom right is a closer look at the sampled transect. The transect was 83% *Typha x glauca* and 17% *T. latifolia*. **b** Ditch site #201 near Minnedosa, MB, 2011. The transect was 100% *T. x glauca*

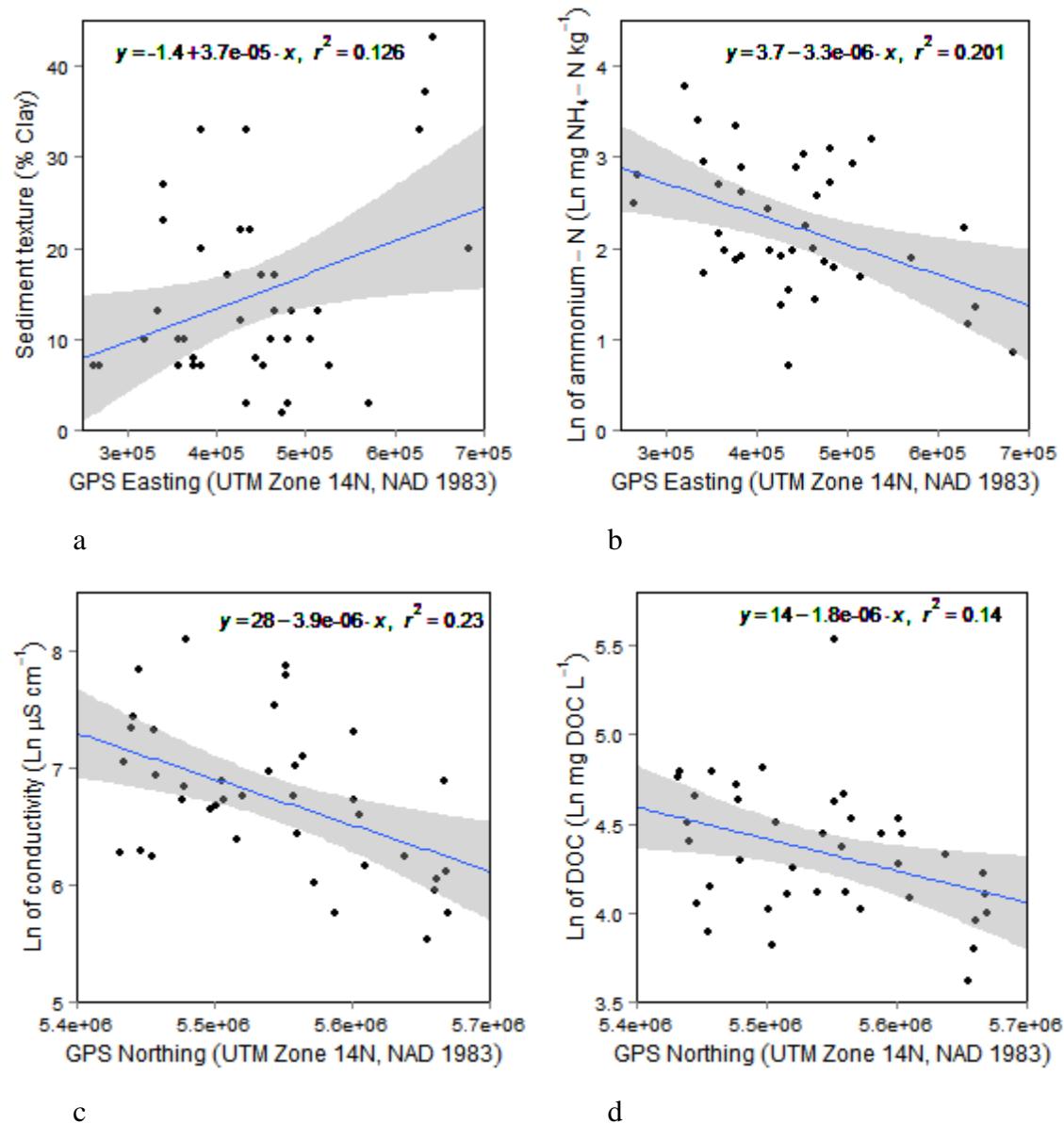


Fig. 3.8 Scatterplots of the statistically significant results of ANOVA linear regression of all combinations of the following environmental variables at pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011: sampling date, GPS easting, GPS northing, \ln of transect length, \ln of water conductivity, pH, \ln of DN, \ln of DOC, sediment texture, \ln of total-N, nitrate-N, \ln of ammonium-N organic-C, and Olsen-P, n=39. **a** GPS Easting versus sediment texture; **b** GPS Easting versus \ln of sediment ammonium-N; **c** GPS Northing versus \ln of water conductivity; **d** GPS Northing versus \ln of water dissolved organic carbon. The 95% confidence intervals were represented by the shaded areas around the lines of best fit. Fig. 3.8 (e) to (q) continued over the next four pages.

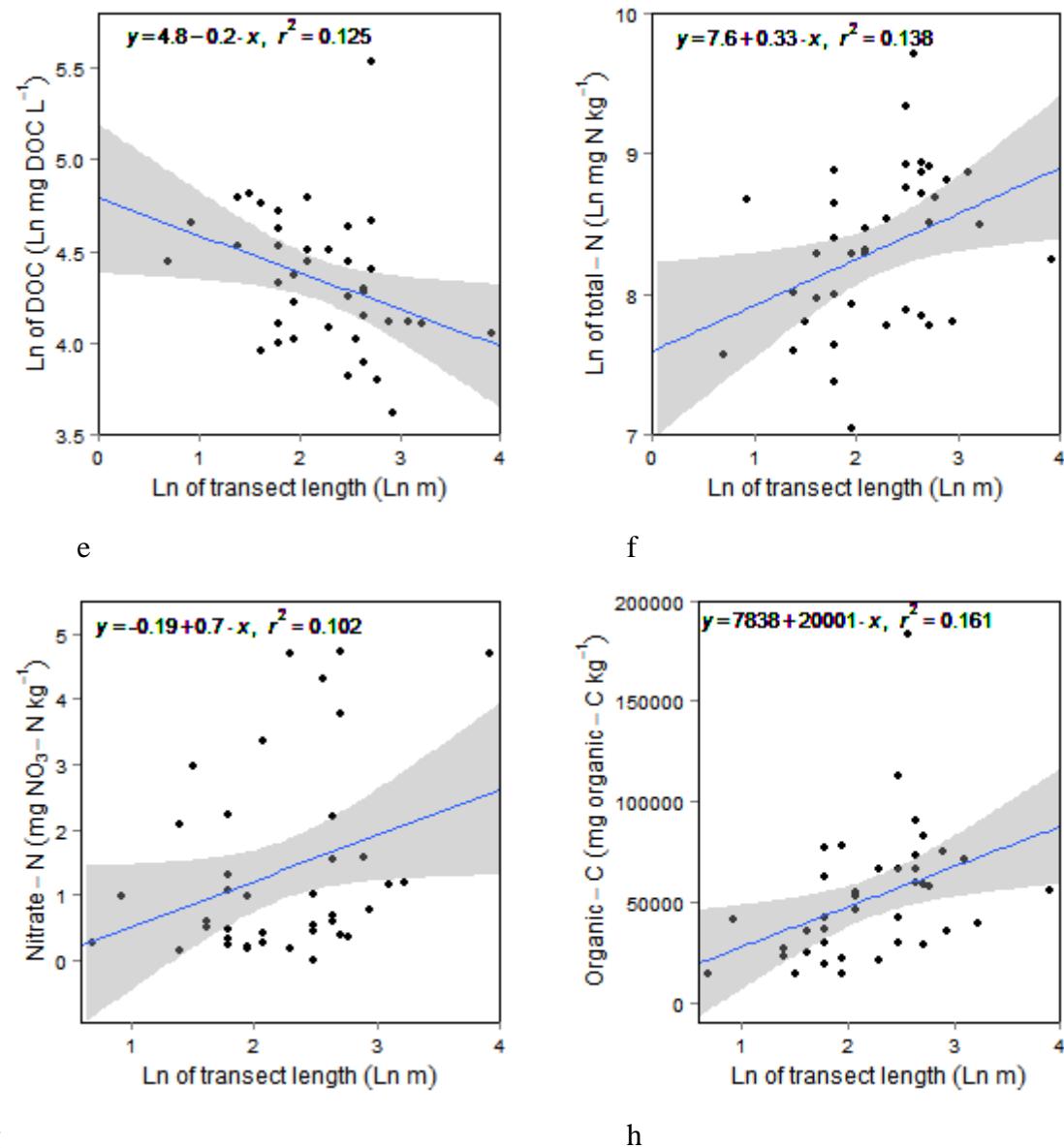


Fig. 3.8 (Continued) **e** \ln of transect length versus \ln of water DOC; **f** \ln of transect length versus \ln of sediment total-N; **g** \ln of transect length versus sediment nitrate-N; **h** \ln of transect length versus sediment organic-C

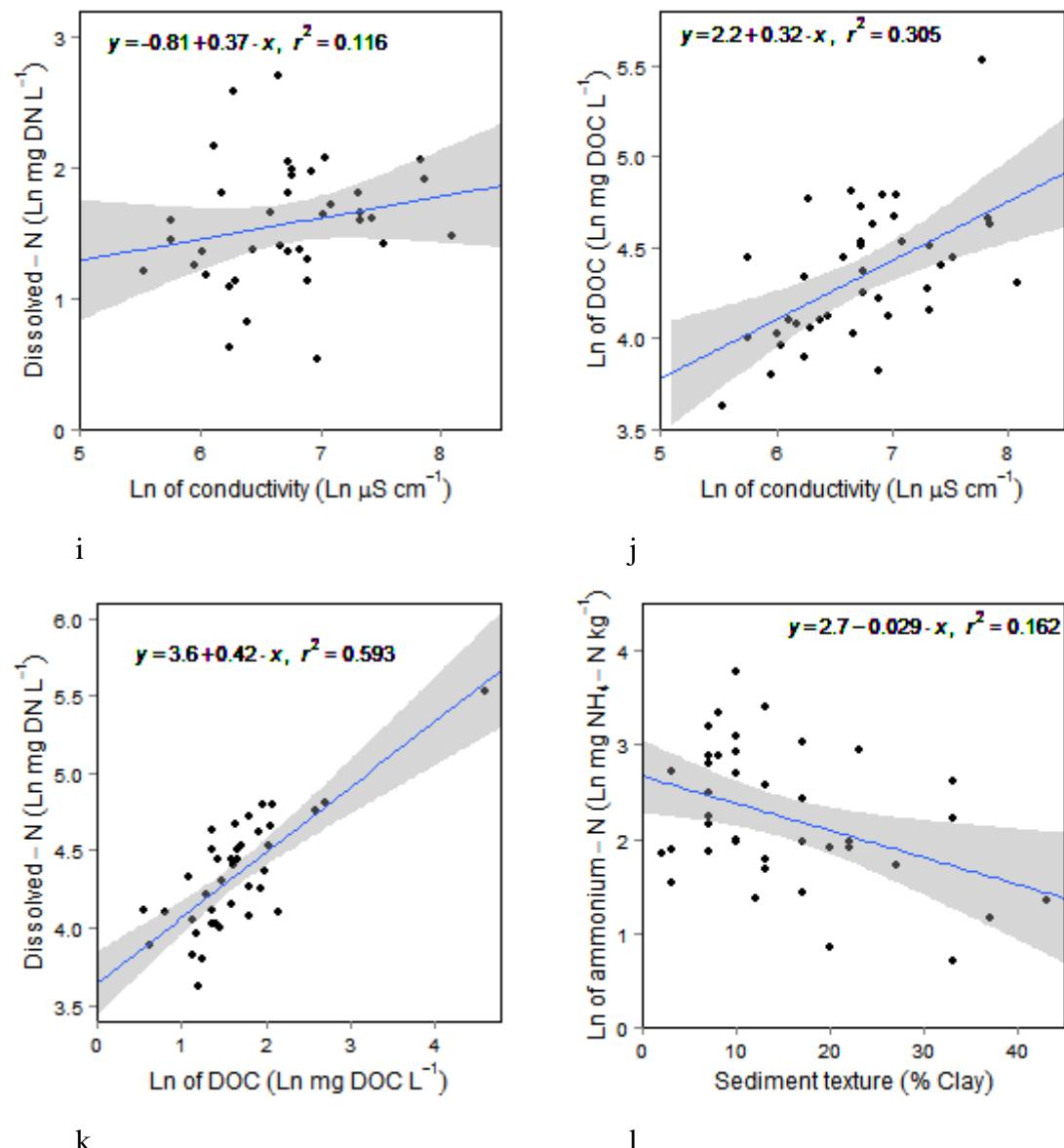


Fig. 3.8 (Continued) **i** Ln of water conductivity versus Ln of water dissolved-N; **j** Ln of water conductivity versus Ln of water DOC; **k** Ln of water DOC versus Ln of water dissolved-N; **l** sediment texture versus the Ln of sediment ammonium-N

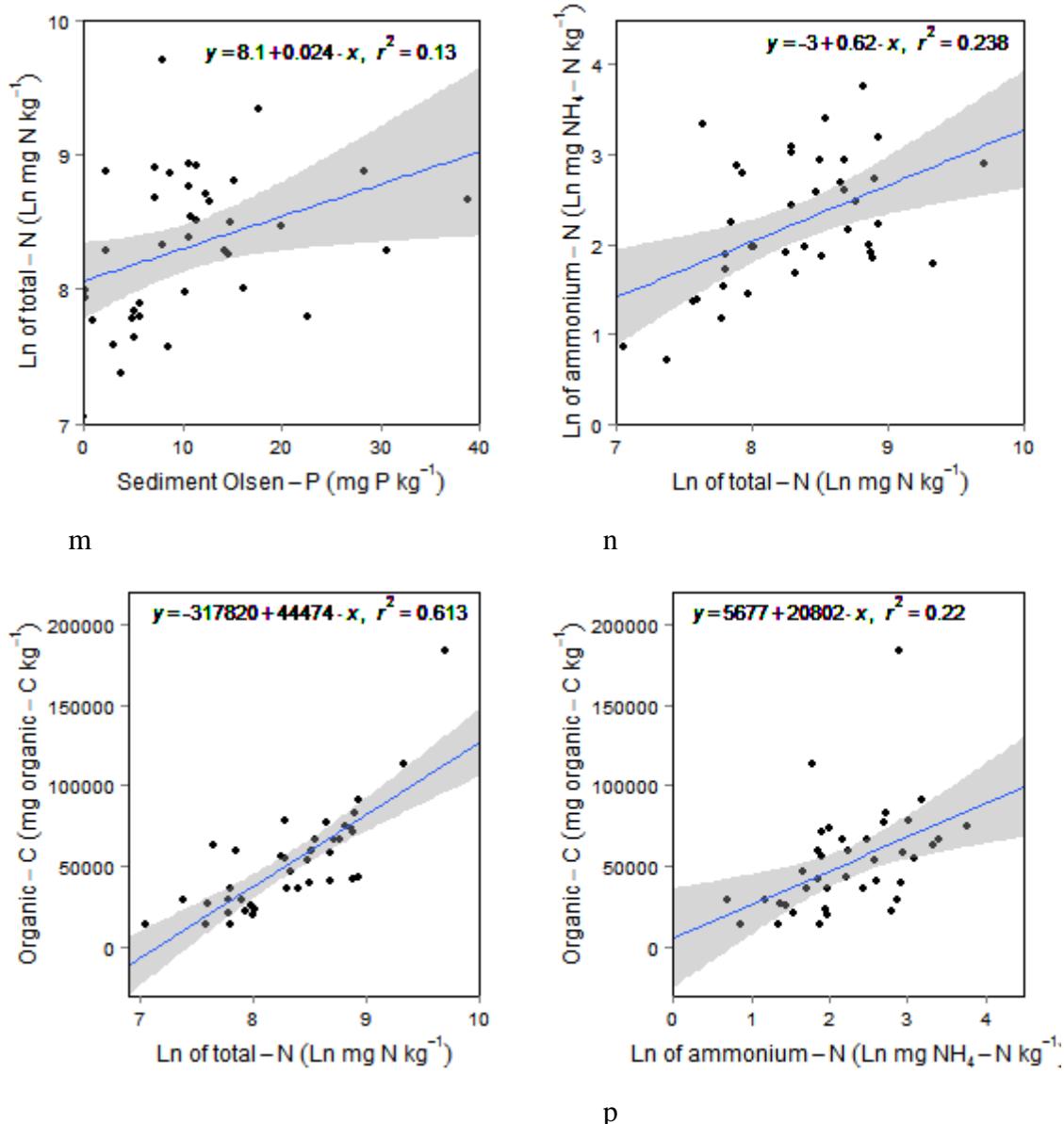


Fig. 3.8 (Continued) **m** Sediment Olsen-P versus \ln of sediment total-N; **n** \ln of sediment total-N versus \ln of sediment ammonium-N; **o** \ln of sediment total-N versus sediment organic-C; **p** \ln of sediment ammonium-N versus sediment organic-C

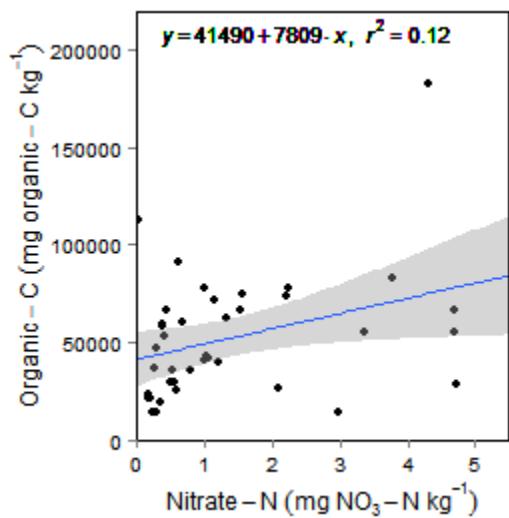


Fig. 3.8 (Continued) q Sediment nitrate-N versus sediment organic-C

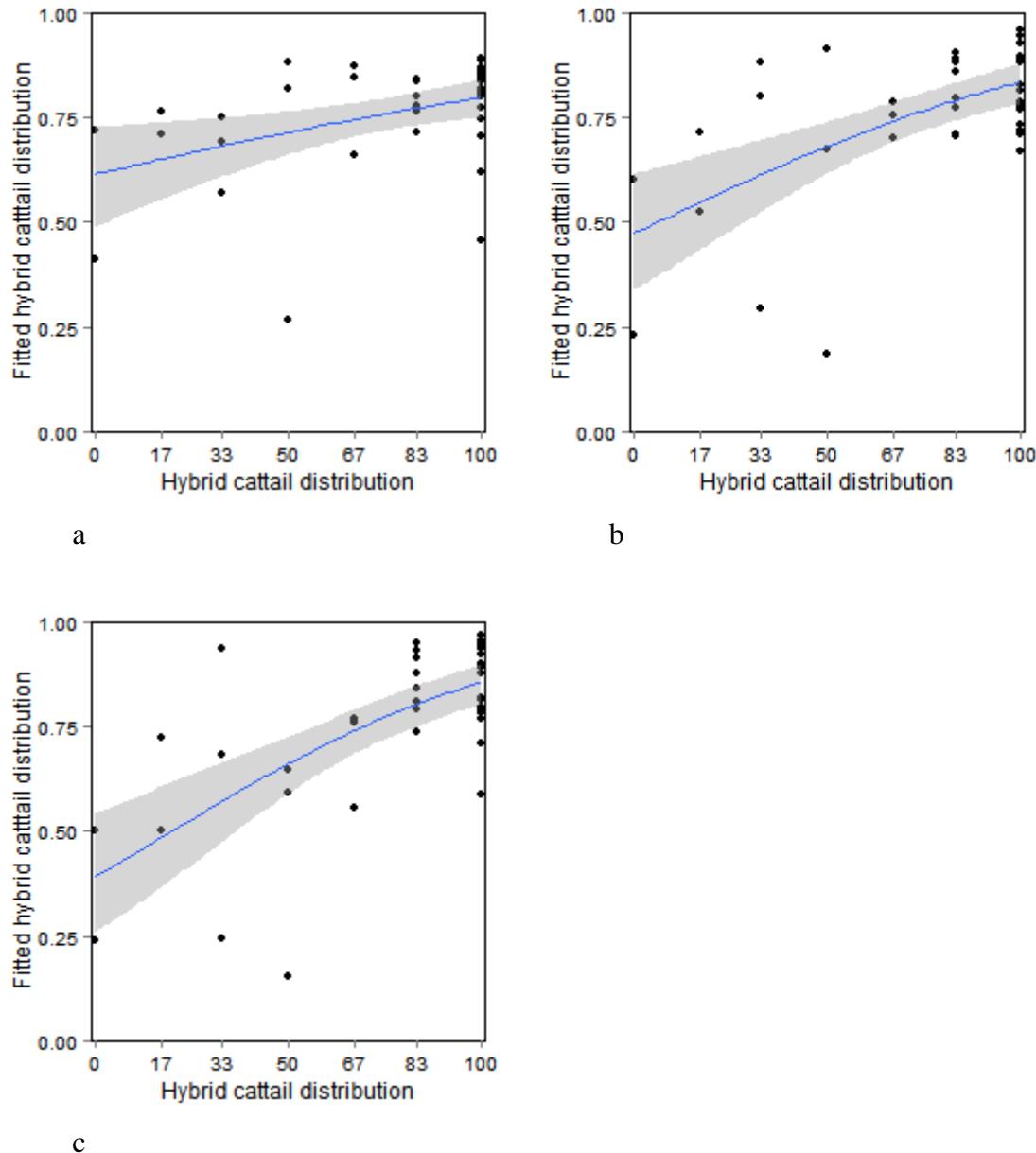


Fig. 3.9 *Typha x glauca* distribution in pothole and ditch marshes in southwestern Manitoba and southeastern Saskatchewan, 2011, versus the *T. x glauca* distribution fitted with the GLM quasi-binomial models, n=39. Where, **a** OlsenP model $\sim \beta_0 + \beta_4\text{OlsenP}$; **b** Full model $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse}$; and **c** FI model $\sim \beta_0 + \beta_3\text{Nitrate} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_3\text{Nitrate}:\beta_4\text{OlsenP}$. The shaded band around the lines of best fit is the 95% confidence interval

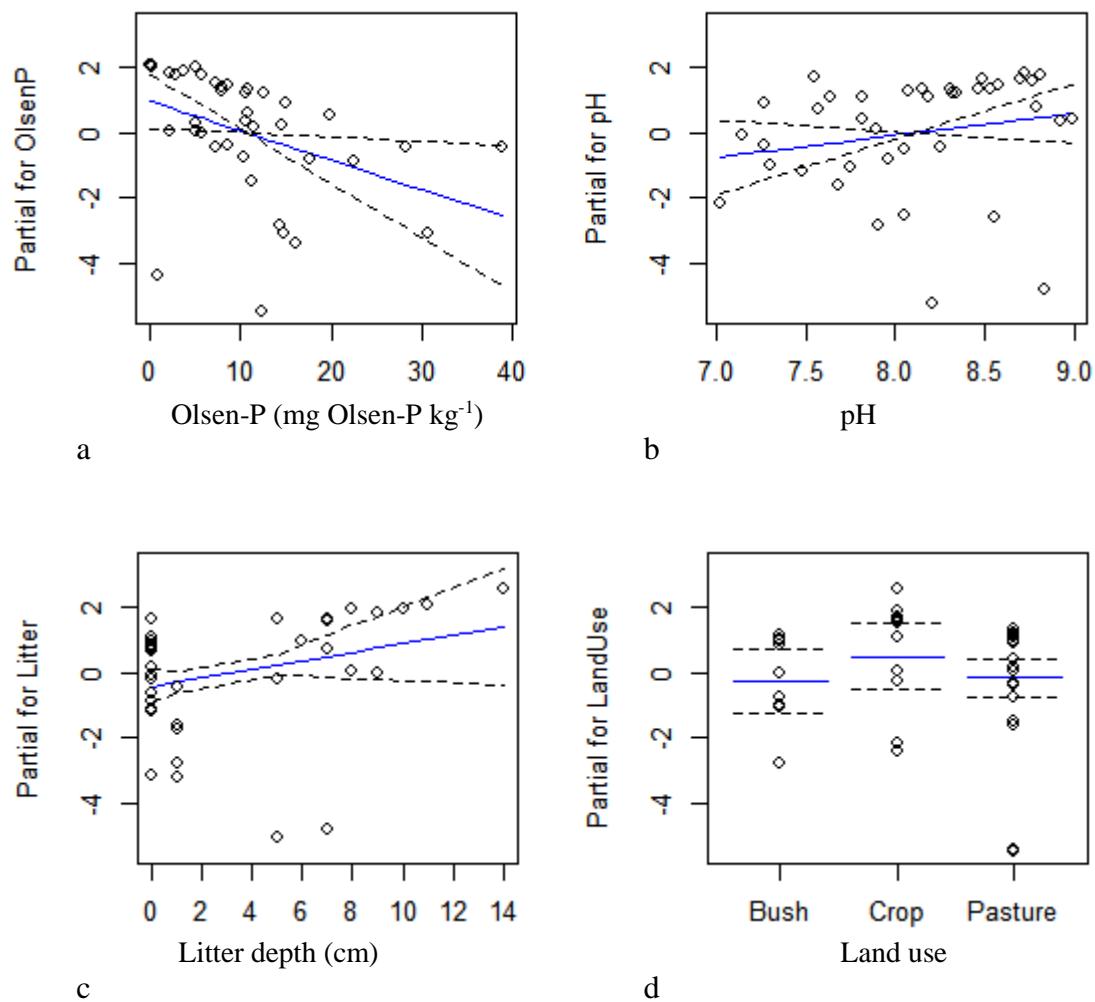


Fig. 3.10 Partial residuals of each predictive term in quasi-binomial GLM Full model of *T. x glauca* distribution in Manitoba and eastern Saskatchewan, 2011. Where Full model $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse}$ Full model $\sim \beta_0 + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse}$. **a** sediment Olsen-P versus partial residuals for Olsen-P; **b** water pH versus partial residuals for pH; **c** mean litter depth versus partial residuals for litter depth; **d** surrounding land use versus partial residuals for land use. The ditto lines around the lines of best fit are the 95% confidence intervals

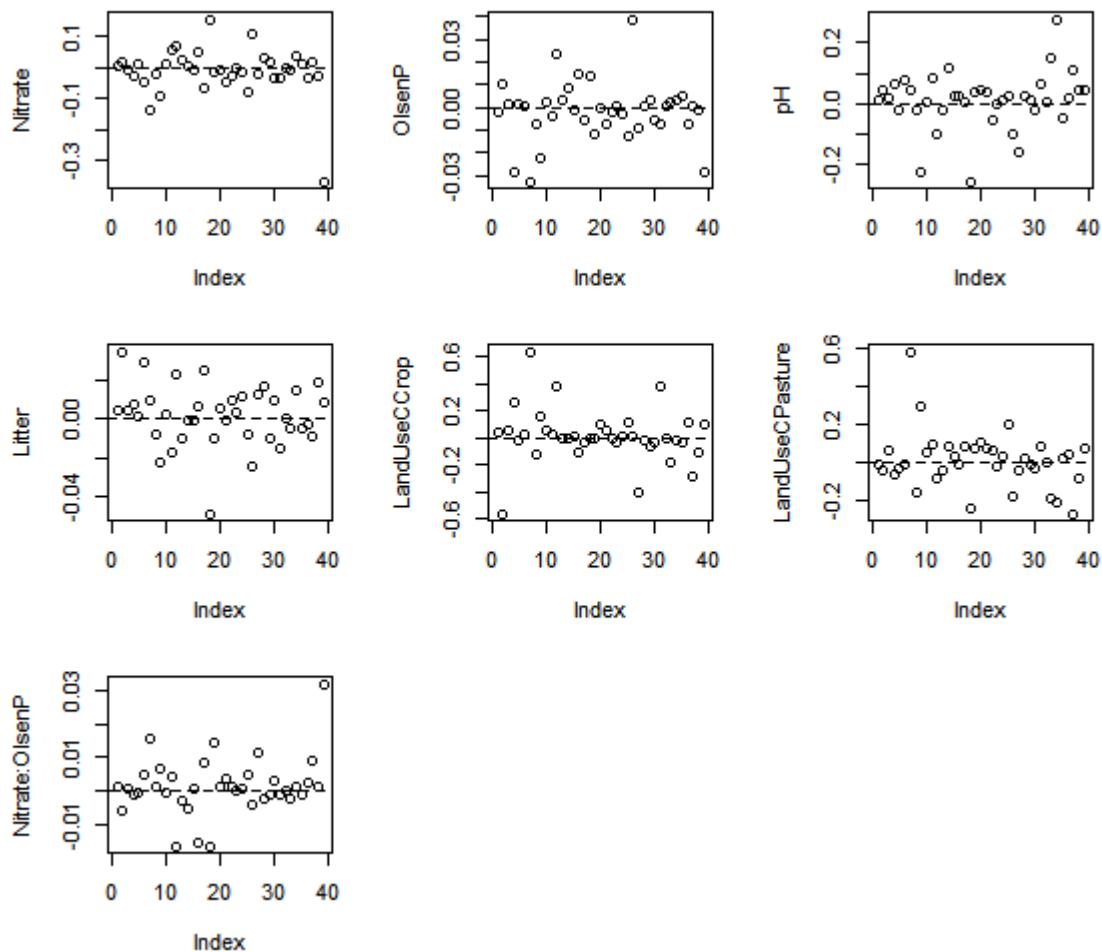


Fig. 3.11 Dfbeta plots of the predictive terms of the FI model for *Typha x glauca* distribution in potholes and ditches in southwestern Manitoba and southeastern Saskatchewan, 2011. Where FI model $\sim \beta_0 + \beta_3\text{Nitrate} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_3\text{Nitrate}:\beta_4\text{OlsenP}$

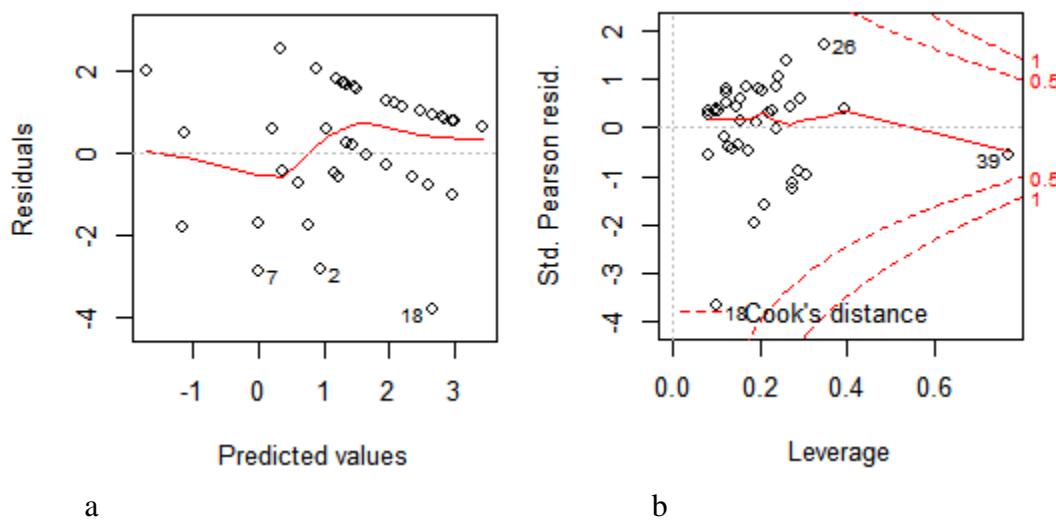


Fig. 3.12 Residual plots of the FI quasi-binomial GLM for *Typha x glauca* distribution in potholes and ditches in southwestern Manitoba and southeastern Saskatchewan, 2011. Where FI model $\sim \beta_0 + \beta_3\text{Nitrate} + \beta_4\text{OlsenP} + \beta_6\text{pH} + \beta_8\text{Litter} + \beta_9\text{LandUse} + \beta_3\text{Nitrate} : \beta_4\text{OlsenP}$. **a** Predicted values versus deviance residuals; **b** leverage versus standardized Pearson residuals

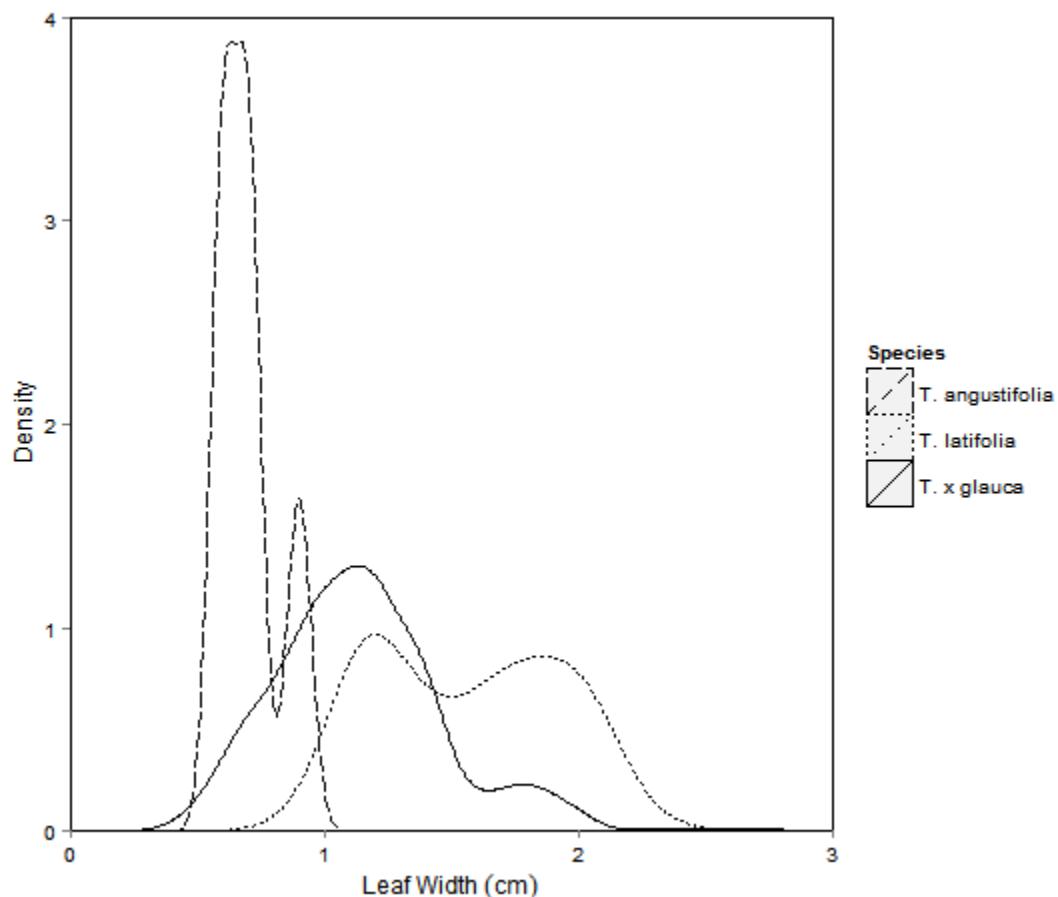


Fig. 3.13 Cumulative frequency distribution of leaf width for 80 *Typha latifolia*, 5 *T. angustifolia*, and 331 *T. x glauca*, collected in southwestern Manitoba and southeastern Saskatchewan prairie pothole, ditch, and lacustrine marshes in 2009 and 2011. The area under each curve is equal to 100% of the distribution sampled for each species. Specimens were identified with the leaf-lamina-margin method adapted from McManus et al. (2002). n = 416

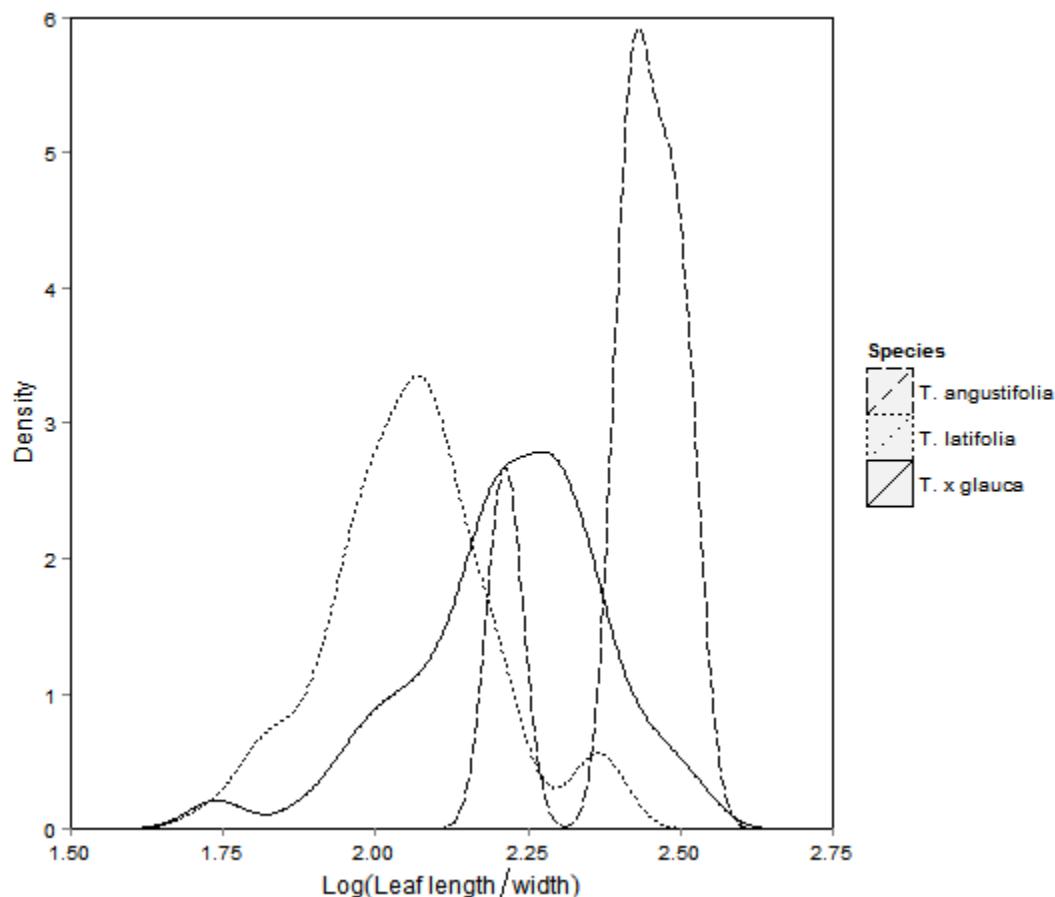


Fig. 3.14 Cumulative frequency distributions of the logarithm of leaf length/ leaf width for 80 *Typha latifolia*, 5 *T. angustifolia*, and 331 *T. x glauca*, collected in southwestern Manitoba and southeastern Saskatchewan prairie pothole, ditch, and lacustrine marshes in 2009 and 2011. The area under each curve is equal to 100% of the distribution sampled for each species. Specimens were identified with the leaf-lamina-margin method adapted from McManus et al. (2002). n = 416

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Chapter 4. Discussion and conclusions on the cattails of southwestern Manitoba and southeastern Saskatchewan

Objectives revisited

At Delta Marsh in 2009, my objectives were (1) to survey the distribution of *Typha latifolia*, *T. angustifolia*, and *T. x glauca* throughout the marsh and to document any differences in their above-ground biomass, density, shoot height, litter biomass, and litter depth; (2) to investigate whether there were any associations between the distribution of the three cattail species and the environmental variables water conductivity, and levels in sediment of texture, Olsen-P, total-N, nitrate-N, and organic-C.

In 2009 in Delta Marsh, the hybrid cattail, *T. x glauca* Godr. was dominant, *T. angustifolia* L. was rare, and *T. latifolia* L. was absent. ANOVA linear regression ($P=0.05$) revealed that above-ground biomass was correlated with mean cattail ramet height, cattail ramet density, and standing litter biomass. Cattail ramet density was negatively correlated with sampling date and positively correlated with standing litter biomass. Mean cattail height was negatively correlated with fallen litter biomass. One-way ANOVA ($P=0.05$) revealed that fallen litter biomass was lowest in quadrats closer to the open water; mean cattail height was greatest at the quadrats closest to the open water; and that mean cattail height was greater in hybrid monoculture than in mixed stands of *T. x glauca* and *T. angustifolia*. Water quality, sediment texture, and sediment chemistry were not associated with the distribution of *T. x glauca*, compared to *T. angustifolia*.

When I expanded the study to prairie pothole and ditch marshes across southwestern Manitoba and into southeastern Saskatchewan in 2011, my objectives were (1) to survey the distribution of *T. latifolia*, *T. angustifolia*, and *T. x glauca* in southwestern Manitoba and southeastern Saskatchewan, and (2) to develop a multivariate model that describes the distribution of cattail species and hybrid in relation to the environmental variables of geographic location, fallen litter depth, surrounding land use, sediment texture and chemistry, and water quality.

Hybrid cattail was most widespread, followed by *T. latifolia*, whereas *T. angustifolia* was only found at one site as far west as central Manitoba. A generalized linear model (GLM) was developed which explained approximately 40% of the variation in *T. x glauca* distribution in the prairie potholes and ditches. The model included the environmental variables of sediment Olsen-P, sediment nitrate-N, water pH, litter depth, surrounding land use, and the interaction variable of Olsen-P:nitrate-N. Olsen-P was the most important of these variables, because its removal from the model reduced significantly the residual deviance of the model ($P=0.05$). Simple logistic regression of hybrid cattail distribution and each potential variable revealed that Olsen-P was the only variable that was correlated with *T. x glauca* distribution on its own ($P=0.05$). The GLM was a poor fit to the data, indicating that either a large portion of the cattail distribution was from chance dispersal or that one or more important variables were missing. Some variables that were not investigated in my study but that could be important in improving the model are wetland age, date of cattail colonization, and hydrology.

T. x glauca was common in pothole and ditch marshes across southwestern Manitoba and southeastern Saskatchewan, forming hybrid cattail monocultures or mixed stands with *T. latifolia*, and forming one mixed stand with *T. angustifolia* in a ditch marsh near Glenboro. Eighteen of the 39 sites analyzed in 2011 were *T. x glauca* monocultures, whereas only two were *T. latifolia* monocultures. *T. x glauca* was dominant at Delta Marsh, a lacustrine marsh, but *T. angustifolia* was also present in this marsh. My study area extended as far west as Yorkton, Saskatchewan, and as far north as Dauphin, Manitoba. The extent of hybrid cattail expansion west and north of my study area has not been reported. Understanding the dynamics between the cattail species and hybrid requires long term survey studies. Conclusions cannot be drawn from this two-year survey as to whether or not the hybrid is displacing *T. latifolia* and *T. angustifolia* in southwestern Manitoba and southeastern Saskatchewan.

Implications for wetland managers and future research

General conclusions cannot be drawn about cattail invasiveness because the correlating factors vary according to location, wetland type, and the extent of anthropogenic disturbances such as agriculture intensity, urbanization, and hydrological changes (Grace and Harrison, 1986; Galatowitsch et al., 1999; Zedler and Kercher, 2004; Olson et al., 2009). Which cattail species are present may also be important for predicting the invasiveness of cattails at specific sites. I found that the distribution of hybrid cattail in comparison with *T. latifolia* was correlated with sediment Olsen-P, sediment nitrate-N, Olsen-P:nitrate-N, litter depth, water pH, and surrounding land use. Therefore, wetland

managers must survey their local conditions to assess how to approach cattail management.

Olsen-P was the most important factor in *T. x glauca* distribution in potholes and ditches in Manitoba and eastern Saskatchewan, although it accounted for only 15% of the variation of the hybrid distribution. This may indicate that the cattails are P-limited in the pothole and ditch marshes in the study area. If the marshes are P-limited, then cattail growth and expansion could be reduced by reducing P concentrations. However, Delta Marsh has been found to be N-limited (Neill, 1990; Bortoluzzi, 2013). Prior to implementing management strategies that regulate nutrient concentrations, it is worthwhile to assess whether nutrients are a major factor in the invasiveness of cattails at a particular site. My study revealed that while nutrient concentration was important for the distribution of hybrid cattail, compared to *T. latifolia*, in pothole and ditch marshes, nutrient concentration was not important to the distribution of hybrid cattail, compared to *T. angustifolia*, in the lacustrine Delta Marsh.

Cattail litter depth was extensive at Delta Marsh, averaging seven cm deep and approximately 700 g m⁻². The litter layer may help to exclude other species and assist its invasion into new territory, as observed at other lacustrine marshes (Farrer and Goldberg, 2009; Vaccaro et al., 2009). Litter depth was also important in the distribution of hybrid cattail in the pothole and ditch marshes surveyed in my study. Hybrid cattail distribution within Delta Marsh was not correlated with sediment chemistry or water quality. Therefore, managing nutrient concentrations alone in Delta Marsh will not likely have any effect on hybrid cattail distribution, in comparison to *T. angustifolia*. Reducing the

litter layer with techniques such as controlled burns could increase other native macrophytes, because litter tends to exclude other species. The stabilization of water levels at Delta Marsh is possibly the most important factor in the dominance of *T. x glauca*, as hypothesized by Shay et al. (1999). The presence of carp in Delta Marsh may also be an important factor for cattail invasiveness, because hybrid cattail invasiveness was correlated with the presence of carp in a lacustrine marsh in Iowa (Egertson et al., 2004). Research into the combined effects of stabilized water levels, litter accumulation and the presence of carp at Delta Marsh is needed.

The persistence of cattails is a challenge for wetland managers. At least two studies have found no evidence of self-thinning in natural cattail stands (Waters and Shay, 1992; Dickerman and Wetzel, 1985). Therefore, once cattail stands are established and dense, they are stable and will likely persist until there is disturbance. *T. x glauca* must be completely removed before native species can be established. In a restoration experiment, if any hybrid cattail remained, it rapidly invaded areas seeded with native vegetation and was expected to out-compete the native flora (Boers et al., 2007).

Expanded survey studies are required to document the rate of cattail expansion in Manitoba and to describe the geographical ranges of *T. latifolia*, *T. angustifolia*, and *T. x glauca*. Genetic analysis is required to decipher whether the hybrids are of the F₁ or later generations. If back-crossing has been involved, identifying which species were involved in the crosses would be beneficial for predicting phenotypes. Because *T. angustifolia* is rare in Manitoba, introgression is more likely to be with *T. latifolia*. To date, the majority of backcrossing identified in the literature has been with *T. angustifolia*, because most

hybrid specimens that were not of the F₁ generation were more genetically similar to *T. angustifolia* than *T. latifolia* (Lee, 1975; Mashburn et al., 1978; Sharitz et al., 1980; Travis et al., 2010; Kirk et al., 2011). However, Kirk et al. (2011), also found a few introgressed individuals that were more genetically similar to *T. latifolia*, which indicates that *T. latifolia* can also be involved in natural back-crosses.

The presence of cattail does not necessarily mean that it is invasive at that location and that all other vegetation will be displaced through time. Bevington (2007) found no difference in biodiversity between *Typha*-dominated stands and stands that were not dominated by cattails in created wetlands that were at least 15 years old. Svengsouk and Mitsch (2001) found that *Schoenoplectus tabernaemontani* was able to compete with *T. x glauca* under low nutrient conditions. The marshes in my broad survey included both extremes of homogenous cattail monocultures and clumps of cattail interspersed within a heterogenous mixture of emergent species. This variation in stand structure may indicate that cattail can co-exist with other emergent species, although the variation in stand structure may also represent variation in cattail colonization date. More research is needed to assess under what conditions each cattail species is invasive. My survey study included litter depth, water quality and sediment chemistry parameters, but it did not include any measures on biodiversity. Revisiting the sites in my study, or a subsample of the sites, and analyzing my data with added biodiversity or species richness measures would provide insight into what conditions are correlated with cattail dominance.

Future research that includes marsh sediment chemistry should use the newer, more accurate in situ resin-P methods. Phosphorus and nitrogen bioavailability in wetland

sediments vary along with the redox potential changes that accompany changes in sediment moisture throughout the season (Mitsch and Gosselink, 2000). These changes are particularly pronounced when sediment goes from anaerobic to aerobic, or vice versa. Experiments on the effects of *T. domingensis* root oxygen stress and phosphorus uptake revealed that the phosphorus uptake by the southern cattail was dependent on the redox potential of the rhizosphere (DeLaune et al., 1999). Sampling methods such as the in situ resin method used by Nelson et al. (2007) more accurately reflect the bioavailability of nutrients such as P and N over time than the methods used in my study.

Accurately identifying cattail to species is important for assessing differences between the species and hybrid. While genetic analysis is accurate, its expense and its requirement for specialized techniques and equipment may be prohibitive for some studies and for routine identification by wetland managers. The identification of characteristics that accurately discriminate between *T. latifolia*, *T. angustifolia*, and *T. x glauca* that are quick, easy, and cost-effective, would benefit researchers and wetland managers because accurate identification is necessary for discriminating functional differences between the cattail species. The leaf-lamina-margin characteristics used in my study offer an alternative to genetic analysis. This method has been validated by one study (McManus et al., 2002), but the method should be validated by other researchers on different cattail populations. Other characters that demonstrate potential for discriminating between species include leaf-apex angle, staminate-spike length, shape of aborted pistil, presence of pistillate bracteoles at the base of pistillate flowers, shape and colour of staminate bracteoles, shape and colour of pistillate hairs, shape of compound pedicel, shape of

stigma, type of pollen, and the seed characters of endosperm width, embryo length, and embryo width (Hotchkiss and Dozier, 1949; Fassett and Calhoun, 1952; Marsh, 1962; Smith, 1967; Lee and Fairbrothers, 1969; Suda et al., 1977; Finkelstein, 2003; Kim et al., 2003). A combination of the log of the ratio of leaf width to leaf length, spike length, spike gap length, and stem diameter identified by Snow et al. (2010) show promise for accurate identification that is more accessible than genetic analysis or microscopy.

My study highlights the complexity of hybrid cattail distribution. Within Manitoba, *T. x glauca* distribution was correlated with sediment Olsen-P, sediment nitrate-N, water pH, litter depth, surrounding land use, and the ratio of nitrate-N:Olsen-P, but only in pothole and ditch marshes. In the lacustrine Delta Marsh none of the environmental variables measured in this study were correlated with *T. x glauca* distribution.

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Appendix A: GPS locations

Table A.1 GPS locations of cattail quadrats along transects at Delta Marsh, 2009. W designates quadrats at the water's edge; M designates quadrats within the middle of the dense band of cattails near the open water; L designates quadrats at the landward edge if the cattail stand. UTM coordinate system, NAD 83, zone 14N.

Transect #	GPSEasting	GPSNorthing	Transect #	GPSEasting	GPSNorthing
1W	542479	5559325	8W	547428	5559167
1M	542488	5559344	8M	547398	5559211
1L	542489	5559344	8L	547326	5559360
2W	545956	5558143	9W	551599	5560015
2W	545955	5558147	9M	551577	5560059
3W	564977	5565419	9L	551507	5560110
3M	564979	5565407	10W	552130	5557543
3L	564979	5565412	10M	552134	5557541
4W	563134	5564765	10L	552136	5557536
4L	563143	5564765	11W	542328	5559389
5W	556921	5562278	11M	542316	5559412
5M	556920	5562279	11L	542299	5559454
5L	556919	5562280	12W	564449	5562625
6W	542391	5558657	12M	564484	5562614
6M	542374	5558649	12L	564489	5562610
6L	542328	5558634	13W	544029	5556156
7W	557809	5562470	13M	544034	5556174
7M	557820	5562490	13L	544038	5556154
7L	557852	5562506			

Table A.2 GPS locations of cattail transects at prairie pothole and roadside ditches in southern Manitoba and eastern Saskatchewan, 2011. UTM coordinate system, NAD 83, zone 14N.

Prairie pothole marshes			Roadside ditch marshes		
Transect #	GPSEasting	GPSNorthing	Transect #	GPSEasting	GPSNorthing
14	443622	5572633	201	426779	5564506
15	506062	5515815	202	382351	5504307
16	474450	5637574	203	383074	5445049
17	451147	5557117	204	413762	5457071
18	375792	5551571	205	479552	5439157
20	426635	5559995	206	464838	5431271
23	412403	5660749	208	682881	5500953
24	433820	5667514	210	438768	5669099
25	453634	5453877	212	569997	5497005
27	433868	5506433	213	641714	5604490
28	479606	5440744	214	375805	5552103
30	464966	5433273	215	341603	5654281
33	460784	5478784	220	364270	5476820
34	484409	5478232	221	357199	5601332
35	526661	5456286	224	514229	5587724
36	383316	5446118	226	633473	5558837
37	320658	5538902			
38	357471	5600889			
40	334066	5609511			
41	341765	5659565			
42	268397	5666811			
43	263489	5543440			
48	627908	5519976			

Appendix B: Calibration curves for chemical analyses

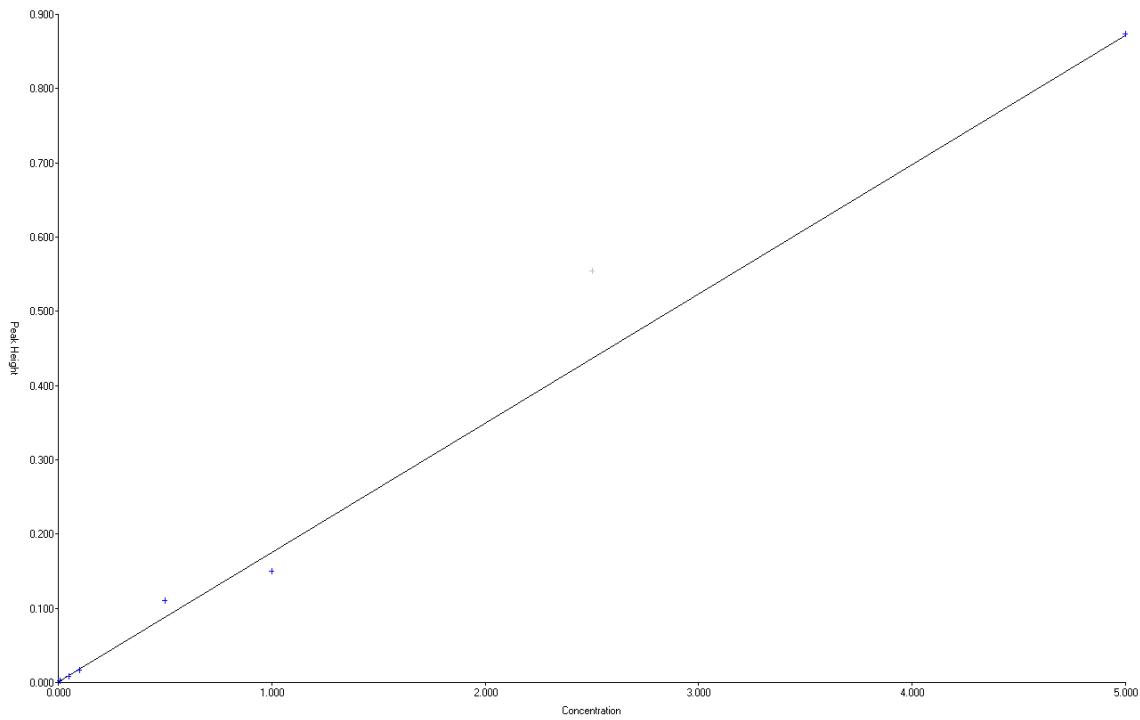


Fig. B.1 Calibration curve for sediment nitrate-N analysis using Astoria 2 spectrophotmeter. Slope = 0.1742, intercept = 0.0002091, correlation = 0.9990

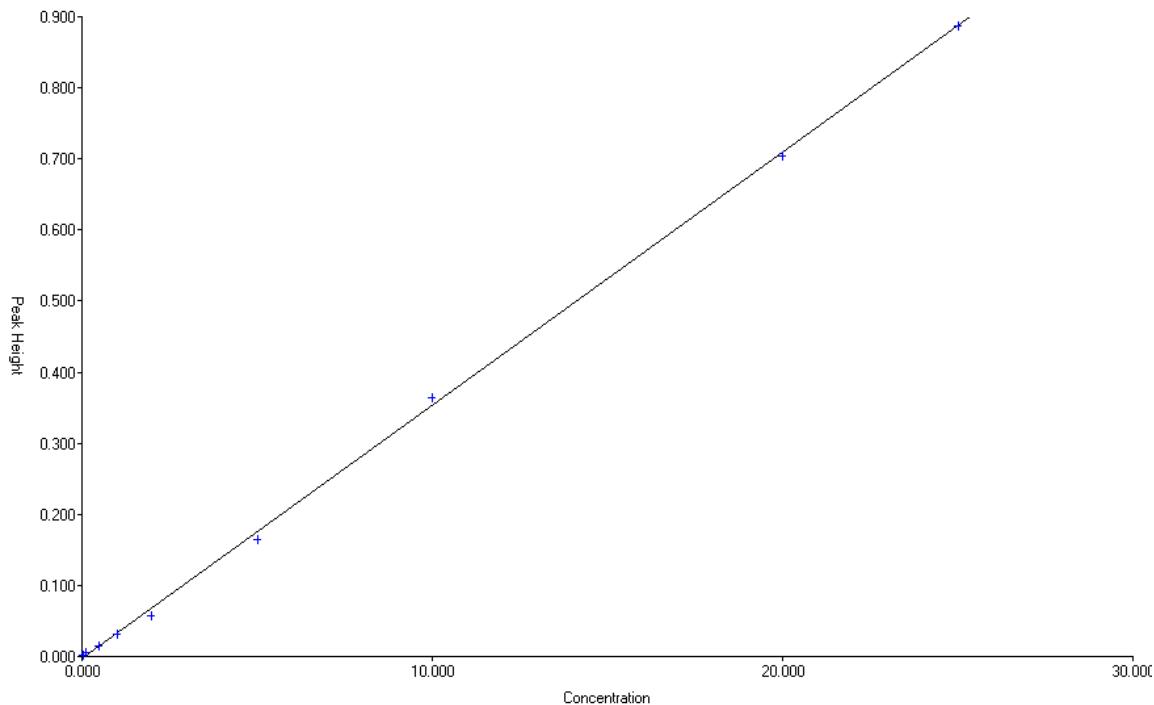


Fig. B.2 Calibration curve for sediment ammonium-N analysis using Astoria 2 spectrophotometer. Slope= 0.02987, intercept = 0.01127, correlation = 0.9982

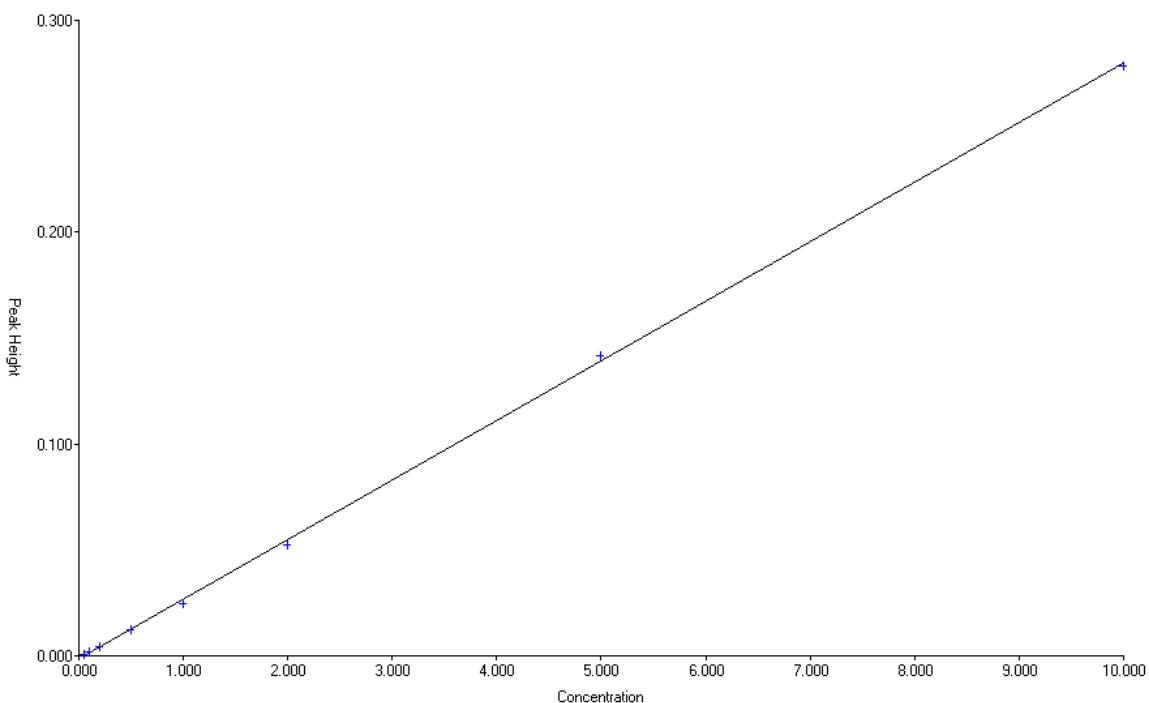


Fig. B.3 Calibration curve for sediment Olsen-P analysis using Astoria 2 spectrophotometer. Slope = 0.02813, intercept = -0.001726, correlation = 0.9999

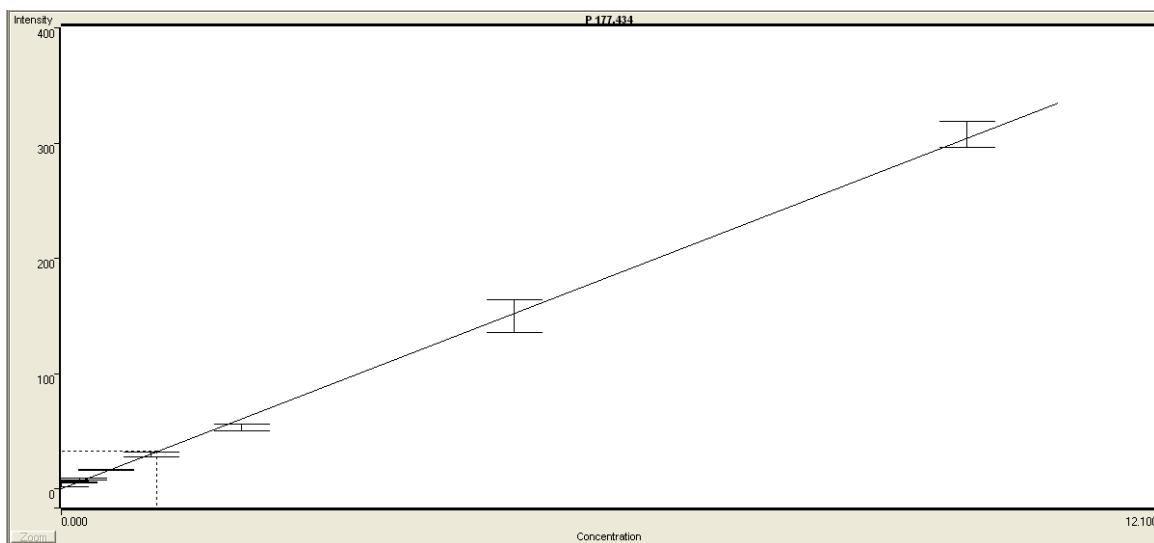


Fig. B.4 Calibration curve for sediment total sodium bicarbonate-extractable P analysis with ICP detected at wavelength 177.434 nm. Correlation = 0.9994

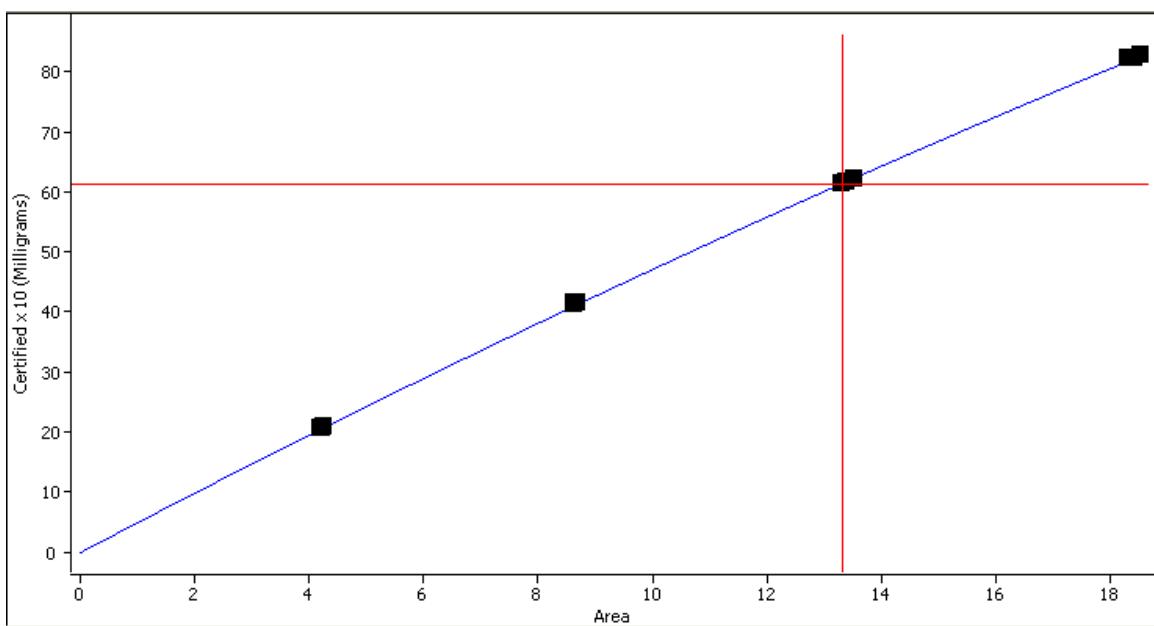


Fig. B.5 Calibration curve for sediment total-C analysis with Leco Tru-Spec. Slope = 0.502635, intercept = -0.00299128, RMS error = 0.12432

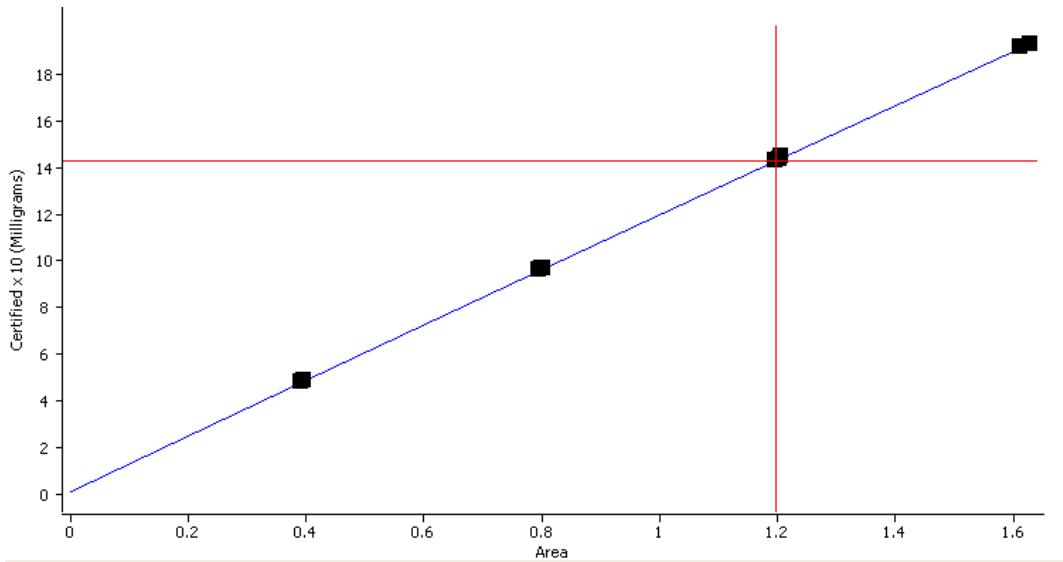


Fig. B.6 Calibration curve for sediment total-N analysis with Leco Tru-Spec. Slope = 1.20439, intercept = -0.0136686, RMS error = 0.041667

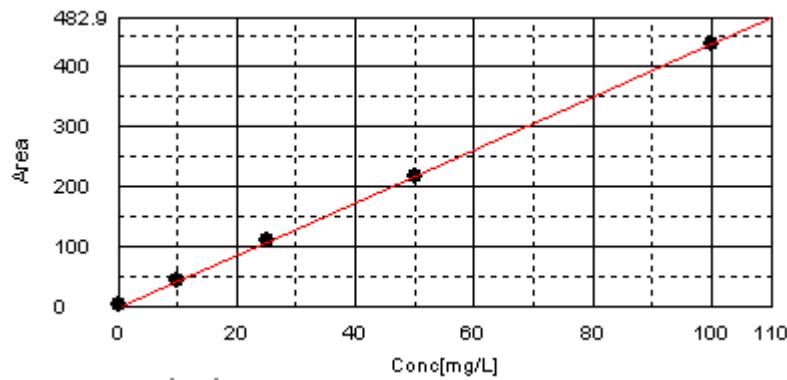


Fig. B.7 Calibration curve for DOC in water analysis with Shimadzu. Slope = 4.390, intercept = -0.9623, $r^2 = 0.9999$

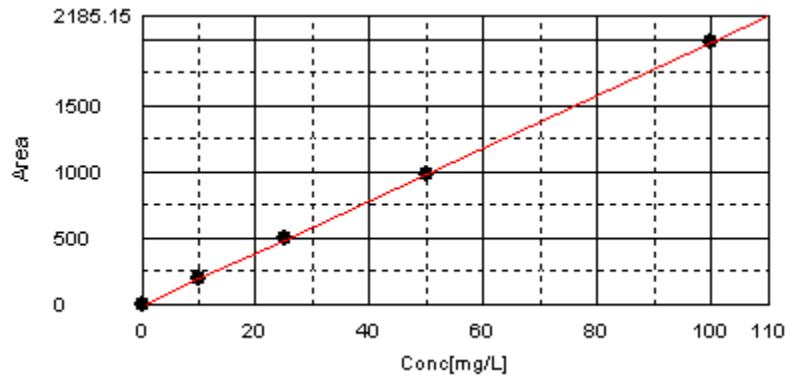


Fig. B.8 Calibration curve for DN in water analysis with Shimadzu. Slope = 19.88, intercept = -5.942, $r^2 = 1.0000$

Appendix C: Files on Accompanying DVD

Table C.1 File location, type, and description of files on DVD of print copy

Folder	File name	File type and program	Description
Main	Wasko_Thesis	Microsoft Word 97 – 2003 Document	Thesis in doc format
Main	Wasko_Thesis	Adobe Acrobat Document	Thesis in pdf format
Main	LeafWidth	Microsoft Excel Comma Separated Values File	Compare leaf widths of cattail spp.
2009Data	2009CattailBiomass	Microsoft Excel Comma Separated Values File	For statistical analysis of biomass data
2009Data	2009DataRaw	Microsoft Excel 97-2003 Worksheet	Raw data and calculations
2009Data	2009DeltaSed	Microsoft Excel Comma Separated Values File	For statistical analysis of sediment data
2011Data	2011FieldPic folder	JPEG pics from cameras	Field pictures in folders by site location
2011Data	2011LeafTipScan folder	JPEG scans	Leaf tip scans for leaf-tip angle analysis
2011Data	2011SiteLocation	Microsoft Excel 97-2003 Worksheet	Location of sites for quick reference
2011Data	2011MicSlidePic folder	JPEG pics from microscope mounted camera	Microscope slides of cattail leaf cross-sections
2011Data	2011Calculations	Microsoft Excel 97-2003 Worksheet	Raw data and calculations
2011Data	2011CattailAll	Microsoft Excel Comma Separated Values File	For statistical analysis of sites with no water
2011Data	2011CattailAllNA	Microsoft Excel Comma Separated Values File	Sites with no water
2011Data	2011FieldData	Microsoft Excel 97-2003 Worksheet	Raw data from field
2011Data	2011Microscope	Microsoft Excel 97-2003 Worksheet	Analysis of microscope slides of cattail leaf cross-sections
2011Data	2011SiteLocation	Microsoft Excel 97-2003 Worksheet	2011 Site locations
2011Data	b7_lab_book	Microsoft Excel 97-2003 Worksheet	Lab analysis for 2009 and 2011
2011Data	env_lab_book	Microsoft Excel 97-2003 Worksheet	Lab analysis for 2009 and 2011

Appendix D: R Code

R code for 2009 cattail biomass analysis at Delta Marsh

```
filePath="C:/Users/Jen/Documents/Cattail/Data/"
fileName=paste(filePath,"2009CattailBiomass.csv",sep="")
DeltaData=read.table(fileName, header=TRUE, sep=",") #import data file

library(car)
library(ggplot2)

palette(gray(seq(.3,.9,len=25))) #change palette to grayscale

Date=(DeltaData$Date)
Date1=(DeltaData$Date1)
Transect=(DeltaData$Transect)
Position=(DeltaData$Position)
Location=(DeltaData$Location)
GPSEasting=(DeltaData$GPSEasting)
GPSNorthing=(DeltaData$GPSNorthing)
Tangustifolia=(DeltaData$Tangustifolia)
TyphaSp=(DeltaData$TyphaSp)
TyphaSp<-as.factor(TyphaSp)
Length=(DeltaData$Length)
FloatingMat=(DeltaData$FloatingMat)
WaterDepth=(DeltaData$WaterDepth)
LitterDepth=(DeltaData$LitterDepth)
LitterDepthMean=(DeltaData$LitterDepthMean)
LitterDepthSTDEV=(DeltaData$LitterDepthSTDEV)
LitterDepthSQRT=(DeltaData$LitterDepthSQRT)
```

Density=(DeltaData\$Density)
DensityMean=(DeltaData\$DensityMean)
DensitySTDEV=(DeltaData\$DensitySTDEV)
DensityLn=(DeltaData\$DensityLn)
DensitySQRT=(DeltaData\$DensitySQRT)
FlowerPercent=(DeltaData\$FlowerPercent)
FlowerPercentMean=(DeltaData\$FlowerPercentMean)
FlowerPercentSTDEV=(DeltaData\$FlowerPercentSTDEV)
FlowerPercentSQRT=(DeltaData\$FlowerPercentSQRT)
Height=(DeltaData\$Height)
HeightMean=(DeltaData\$HeightMean)
HeightSTDEV=(DeltaData\$HeightSTDEV)
DensityHeight=(DeltaData\$DensityHeight)
Width=(DeltaData\$Width)
WidthMean=(DeltaData\$WidthMean)
WidthSTDEV=(DeltaData\$WidthSTDEV)
DHW=(DeltaData\$DHW)
LNDHW=(DeltaData\$LNDHW)
NFBiomass=(DeltaData\$NFBiomass)
NFBiomassMean=(DeltaData\$NFBiomassMean)
NFBiomassSTDEV=(DeltaData\$NFBiomassSTDEV)
NFBiomassSQRT=(DeltaData\$NFBiomassSQRT)
FBiomass=(DeltaData\$FBiomass)
FBiomassMean=(DeltaData\$FBiomassMean)
FBiomassSTDEV=(DeltaData\$FBiomassSTDEV)
FBiomassSQRT=(DeltaData\$FBiomassSQRT)
TotalBiomass=(DeltaData\$TotalBiomass)
TotalBiomassMean=(DeltaData\$TotalBiomassMean)
TotalBiomassSTDEV=(DeltaData\$TotalBiomassSTDEV)
TotalBiomassSQRT=(DeltaData\$TotalBiomassSQRT)
BiomassSLitter=(DeltaData\$BiomassSLitter)

```

BiomassSLitterSQRT=(DeltaData$BiomassSLitterSQRT)
BiomassSLitterMean=(DeltaData$BiomassSLitterMean)
BiomassSLitterSTDEV=(DeltaData$BiomassSLitterSTDEV)
BiomassFLitter=(DeltaData$BiomassFLitter)
BiomassFLitterSQRT=(DeltaData$BiomassFLitterSQRT)
BiomassFLitterMean=(DeltaData$BiomassFLitterMean)
BiomassFLitterSTDEV=(DeltaData$BiomassFLitterSTDEV)

summary(DeltaData)
boxplot(NFBiomass, horizontal=TRUE)
boxplot(NFBiomassSQRT, horizontal=TRUE)
boxplot(FBiomass, horizontal=TRUE)
boxplot(FBiomassSQRT, horizontal=TRUE)
boxplot(TotalBiomass, horizontal=TRUE)
boxplot(TotalBiomassSQRT~Location, horizontal=TRUE)
boxplot(FlowerPercent, horizontal=TRUE)
boxplot(FlowerPercentSQRT, horizontal=TRUE)
boxplot(LitterDepth, horizontal=TRUE)
boxplot(LitterDepthSQRT, horizontal=TRUE)
boxplot(Height, horizontal=TRUE)
boxplot(BiomassFLitter, horizontal=TRUE)
boxplot(BiomassFLitterSQRT, horizontal=TRUE)
boxplot(BiomassSLitter, horizontal=TRUE)
boxplot(BiomassSLitterSQRT, horizontal=TRUE)
boxplot(Density, horizontal=TRUE)
boxplot(DensityLn, horizontal=TRUE)
boxplot(DensitySQRT, horizontal=TRUE)

par(mar=c(4,1,1,1), mfrow=c(4,2), family="serif", cex=0.8)
boxplot(TotalBiomass, horizontal=TRUE,
       xlab=expression((a)~Total~biomass~("g m"^-2)))

```

```

boxplot(TotalBiomassSQRT, horizontal=TRUE,
        xlab=expression((b)~Square~root~total~biomass~(sqrt("g m"^-2))))
boxplot(NFBiomass, horizontal=TRUE,
        xlab=expression((c)~Non-flowering~biomass~("g m"^-2)))
boxplot(NFBiomassSQRT, horizontal=TRUE,
        xlab=expression((d)~Square~root~non-flowering~biomass~(sqrt("g m"^-2))))
boxplot(BiomassSLitter, horizontal=TRUE,
        xlab=expression((e)~Standing~litter~biomass~("g m"^-2)))
boxplot(BiomassSLitterSQRT, horizontal=TRUE,
        xlab=expression((f)~Square~root~standing~litter~biomass~(sqrt("g m"^-2))))
boxplot(LitterDepth, horizontal=TRUE,
        xlab=expression((g)~Litter~depth~(cm)))
boxplot(LitterDepthSQRT, horizontal=TRUE,
        xlab=expression((h)~Square~root~litter~depth~(sqrt(cm))))


par(mar=c(4,3,1,1), mfrow=c(3,2), family="serif", cex=0.8)
boxplot(Density~Location, horizontal=TRUE,
        xlab=expression((a)~Cattail~density~("shoots m"^-2)))
boxplot(Height~Location, horizontal=TRUE,
        xlab=expression((b)~Mean~cattail~height~(cm)))
boxplot(TotalBiomassSQRT~Location, horizontal=TRUE,
        xlab=expression((c)~Square~root~total~biomass~(sqrt("g m"^-2))))
boxplot(BiomassSLitterSQRT~Location, horizontal=TRUE,
        xlab=expression((e)~Square~root~standing~litter~biomass~(sqrt("g m"^-2))))
boxplot(BiomassFLitter~Location, horizontal=TRUE,
        xlab=expression((e)~Fallen~litter~biomass~("g m"^-2)))
boxplot(LitterDepthSQRT~Location, horizontal=TRUE,
        xlab=expression((f)~Square~root~litter~depth~(sqrt(cm))))


scatterplotMatrix(~TotalBiomassSQRT + NFBiomassSQRT + FBiomassSQRT +
    BiomassSLitter + BiomassFLitter + DensityHeight + LNDHW +

```

```
DHW + Density + LitterDepth + FlowerPercentSQRT + Height +
Date,
data=DeltaData, diagonal=c("boxplot"), reg.line=FALSE, smooth=FALSE,
transform=FALSE, cex.labels=0.75)
```

```
scatterplotMatrix(~TotalBiomassSQRT + NFBiomassSQRT + FBiomassSQRT +
BiomassSLitter + BiomassFLitter + Density +
LitterDepthSQRT + FlowerPercentSQRT + Height + Date,
data=DeltaData, diagonal=c("boxplot"), reg.line=lm, smooth=FALSE,
transform=FALSE, cex.labels=0.75)
cor.test(TotalBiomassSQRT, Height, method=c("pearson"))
cor.test(TotalBiomassSQRT, Density, method=c("pearson"))
cor.test(TotalBiomassSQRT, LitterDepthSQRT, method=c("pearson"))
cor.test(TotalBiomassSQRT, BiomassSLitterSQRT, method=c("pearson"))
cor.test(TotalBiomassSQRT, BiomassFLitter, method=c("pearson"))
cor.test(LitterDepthSQRT, BiomassFLitter, method=c("pearson"))
```

```
lmBiomassDate<-lm(TotalBiomassSQRT~Date)
summary(lmBiomassDate)
anova(lmBiomassDate)
```

```
lmSLitterDate<-lm(BiomassSLitterSQRT~Date)
summary(lmSLitterDate)
anova(lmSLitterDate)
```

```
lmFLitterDate<-lm(BiomassFLitter~Date)
summary(lmFLitterDate)
anova(lmFLitterDate)
```

```
lmLitterDepthDate<-lm(LitterDepthSQRT~Date)
summary(lmLitterDepthDate)
```

```
anova(lmLitterDepthDate)
```

```
lmDensityDate<-lm(Density~Date)  
summary(lmDensityDate)  
anova(lmDensityDate)
```

```
lmDateDensity<-lm(Date~Density)  
summary(lmDateDensity)  
anova(lmDateDensity)
```

```
lmHeightDate<-lm(Height~Date)  
summary(lmHeightDate)  
anova(lmHeightDate)
```

```
lmBiomassSLitter<-lm(TotalBiomassSQRT~BiomassSLitterSQRT)  
summary(lmBiomassSLitter)  
anova(lmBiomassSLitter)
```

```
lmBiomassFLitter<-lm(TotalBiomassSQRT~BiomassFLitter)  
summary(lmBiomassFLitter)  
anova(lmBiomassFLitter)
```

```
lmBiomassDepth<-lm(TotalBiomassSQRT~LitterDepthSQRT)  
summary(lmBiomassDepth)  
anova(lmBiomassDepth)
```

```
lmBiomassHeight<-lm(TotalBiomassSQRT~Height)  
summary(lmBiomassHeight)  
anova(lmBiomassHeight)
```

```
lmBiomassDensity<-lm(TotalBiomassSQRT~Density)
summary(lmBiomassDensity)
anova(lmBiomassDensity)
```

```
lmBiomassDensityDate<-lm(TotalBiomassSQRT~Density + Date + Density*Date)
summary(lmBiomassDensityDate)
anova(lmBiomassDensityDate)
```

```
lmDensitySLitter<-lm(Density~BiomassSLitterSQRT)
summary(lmDensitySLitter)
anova(lmDensitySLitter)
```

```
lmDensityFLitter<-lm(Density~BiomassFLitter)
summary(lmDensityFLitter)
anova(lmDensityFLitter)
```

```
lmDensityDepth<-lm(Density~LitterDepthSQRT)
summary(lmDensityDepth)
anova(lmDensityDepth)
```

```
lmDensityHeight<-lm(Density~Height)
summary(lmDensityHeight)
anova(lmDensityHeight)
```

```
lmHeightFlitter<-lm(Height~BiomassFLitter)
summary(lmHeightFlitter)
anova(lmHeightFlitter)
```

```
lmFLitterDepth<-lm(BiomassFLitter~LitterDepthSQRT)
summary(lmFLitterDepth)
anova(lmFLitterDepth)
```

```
lmFLitterSLitter<-lm(BiomassFLitter~BiomassSLitterSQRT)
```

```
summary(lmFLitterSLitter)
```

```
anova(lmFLitterSLitter)
```

```
lmHeightSLitter<-lm(Height~BiomassSLitterSQRT)
```

```
summary(lmHeightSLitter)
```

```
anova(lmHeightSLitter)
```

```
lmSLitterDepth<-lm(BiomassSLitterSQRT~LitterDepthSQRT)
```

```
summary(lmSLitterDepth)
```

```
anova(lmSLitterDepth)
```

```
lmHeightDepth<-lm(Height~LitterDepthSQRT)
```

```
summary(lmHeightDepth)
```

```
anova(lmHeightDepth)
```

```
leveneTest(TotalBiomassSQRT,Location, center=mean)
```

```
BiomassLocation<-aov(TotalBiomassSQRT~Location)
```

```
summary(BiomassLocation)
```

```
leveneTest(BiomassSLitterSQRT,Location, center=mean)
```

```
SLitterLocation<-aov(BiomassSLitterSQRT~Location)
```

```
summary(SLitterLocation)
```

```
leveneTest(BiomassFLitter,Location, center=mean)
```

```
FLitterLocation<-aov(BiomassFLitter~Location)
```

```
summary(FLitterLocation)
```

```
leveneTest(Density,Location, center=mean)
```

```
DensityLocation<-aov(Density~Location)
```

```
summary(DensityLocation)
```

```
leveneTest(Height, Location, center=mean)
```

```
HeightLocation<-aov(Height~Location)
```

```
summary(HeightLocation)
```

```
leveneTest(LitterDepthSQRT, Location, center=mean)
```

```
LitterDepthLocation<-aov(LitterDepthSQRT~Location)
```

```
summary(LitterDepthLocation)
```

```
leveneTest(TotalBiomassSQRT, Position, center=mean)
```

```
BiomassPosition<-aov(TotalBiomassSQRT~Position)
```

```
summary(BiomassPosition)
```

```
leveneTest(BiomassSLitterSQRT, Position, center=mean)
```

```
SLitterPosition<-aov(BiomassSLitterSQRT~Position)
```

```
summary(SLitterPosition)
```

```
leveneTest(BiomassFLitter, Position, center=mean)
```

```
FLitterPosition<-aov(BiomassFLitter~Position)
```

```
summary(FLitterPosition)
```

```
leveneTest(Density, Position, center=mean)
```

```
DensityPosition<-aov(Density~Position)
```

```
summary(DensityPosition)
```

```
leveneTest(Height, Position, center=mean)
```

```
HeightPosition<-aov(Height~Position)
```

```
summary(HeightPosition)
```

```
leveneTest(LitterDepthSQRT, Position, center=mean)
```

```

LitterDepthPosition<-aov(LitterDepthSQRT~Position)
summary(LitterDepthPosition)

ggplot(DeltaData, aes(x=Date, y=Density)) +
  xlab("Sampling date") +
  ylab(expression(Cattail~density~("shoots m"^-2))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_y_continuous(limits=c(0, 130), breaks = c(0, 25, 50, 75, 100, 125)) +
  scale_x_continuous(expand = c(0,0), limits = c(40000,40033), breaks = c(40001, 40008,
  40015, 40022, 40029), labels=c("Jul 7", "Jul 14", "Jul 21", "Jul 28", "Aug 4")) +
  geom_text(data=NULL, x=40025, y=128, label="y=34408 - 0.86x", colour="black",
  size=4) +
  theme(axis.line = element_line(colour = "black"),
  axis.text=element_text(colour="black"),
  panel.grid.major = element_blank(),
  panel.grid.minor = element_blank(),
  panel.border = element_blank(),
  panel.background = element_rect(colour="black", fill="NA"))

ggplot(DeltaData, aes(x=BiomassSLitterSQRT, y=TotalBiomassSQRT)) +
  xlab(expression(SQRT~standing~litter~biomass~(sqrt("g m"^-2)))) +
  ylab(expression(SQRT~total~biomass~(sqrt("g m"^-2)))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_y_continuous(expand=c(0,0), limits=c(8, 53)) +
  scale_x_continuous(expand = c(0,0), limits = c(-2.5,44)) +
  geom_text(data=NULL, x=10, y=50, label="y=22.0 + 0.271x", colour="black", size=4) +
  theme(axis.line = element_line(colour = "black"),
  axis.text=element_text(colour="black"),
  panel.grid.major = element_blank(),
  panel.grid.minor = element_blank(),
  panel.border = element_blank(),
  panel.background = element_rect(colour="black", fill="NA"))

```

```

ggplot(DeltaData, aes(x=Height, y=TotalBiomassSQRT)) +
  xlab(expression(Mean~shoot~height~(cm))) +
  ylab(expression(SQRT~total~biomass~(sqrt("g m"^-2)))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_y_continuous(expand=c(0,0), limits=c(8, 53)) +
  scale_x_continuous(expand = c(0,0), limits = c(50,325), breaks =
c(50,100,150,200,250,300)) +
  geom_text(data=NULL, x=125, y=50, label="y=9.8 + 0.10x", colour="black", size=4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(DeltaData, aes(x=Density, y=TotalBiomassSQRT)) +
  xlab(expression(Cattail~density~("shoots m"^-2))) +
  ylab(expression(SQRT~total~biomass~(sqrt("g m"^-2)))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_y_continuous(expand=c(0,0), limits=c(0, 60), breaks=seq(0,60,10)) +
  scale_x_continuous(expand = c(0,0), limits = c(0,130)) +
  geom_text(data=NULL, x=40, y=57, label="y=16.4 + 0.192x", colour="black", size=4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(DeltaData, aes(x=BiomassSLitterSQRT, y=Density)) +

```

```

ylab(expression(Cattail~density~("shoots m"^-2))) +
xlab(expression(SQRT~standing~litter~biomass~(sqrt("g m"^-2)))) +
geom_point() + geom_smooth(method="lm", fullrange=TRUE) +
scale_x_continuous(expand=c(0,0), limits = c(-1,40)) +
scale_y_continuous(expand=c(0,0), limits=c(0, 125), breaks = c(0, 25, 50, 75, 100, 125)) +
geom_text(data=NULL, x=31, y=118, label="y=41.3 + 0.739x", colour="black",
size=4)+

theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(DeltaData, aes(x=BiomassFLitter, y=Height)) +
ylab(expression(Mean~shoot~height~(cm))) +
xlab(expression(Fallen~litter~biomass~("g m"^-2))) + geom_point() +
geom_smooth(method="lm", fullrange=TRUE) +
scale_x_continuous(expand=c(0,0), limits=c(-50, 1750)) +
scale_y_continuous(expand = c(0,0), limits = c(50,275), breaks =
c(50,100,150,200,250)) +
geom_text(data=NULL, x=1400, y=260, label="y=199-0.039x", colour="black",
size=4)+

theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(DeltaData, aes(x=LitterDepthSQRT, y=BiomassFLitter)) +

```

```

xlab(expression(Square~root~litter~depth~(sqrt(cm)))) +
ylab(expression(Fallen~litter~biomass~("g m"^-2))) + geom_point() +
geom_smooth(method="lm", fullrange=TRUE) +
scale_x_continuous(expand=c(0,0), limits=c(0, 5.7)) +
scale_y_continuous(expand = c(0,0), limits = c(-275,2000)) +
geom_text(data=NULL, x=1.5, y=1850, label="y=-3.22+297x", colour="black",
size=4)+

theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

leveneTest(TotalBiomassSQRT,TyphaSp, center=mean)
TyphaBiomass<-aov(TotalBiomassSQRT~TyphaSp)
summary(TyphaBiomass)

leveneTest(BiomassSLitterSQRT,TyphaSp, center=mean)
TyphaSLitter<-aov(BiomassSLitterSQRT~TyphaSp)
summary(TyphaSLitter)

leveneTest(BiomassFLitter,TyphaSp, center=mean)
TyphaFLitter<-aov(BiomassFLitter~TyphaSp)
summary(TyphaFLitter)

leveneTest(Density,TyphaSp, center=mean)
TyphaDensity<-aov(Density~TyphaSp)
summary(TyphaDensity)

leveneTest(Height,TyphaSp, center=mean)

```

```

TyphaHeight<-aov(Height~TyphaSp)
summary(TyphaHeight)

leveneTest(LitterDepthSQRT,TyphaSp, center=mean)
TyphaLitterDepth<-aov(LitterDepthSQRT~TyphaSp)
summary(TyphaLitterDepth)

par(mfrow=c(1,1), mar=c(4.5,4.5,1,1),family="serif")
boxplot(BiomassFLitter~Position, xlab="Quadrat position along transect",
       ylab=expression(Fallen~litter~biomass~("g m"^-2)))

par(mfrow=c(1,1), mar=c(4.5,4.5,1,1),family="serif")
boxplot(Height~Position, xlab="Quadrat position along transect",
       ylab=expression(Mean~cattail~height~(cm)))

par(mfrow=c(1,1), mar=c(4.5,4.5,1,1),family="serif")
boxplot(Height~TyphaSp, xlab="Cattail stand type",
       ylab=expression(Mean~cattail~height~(cm)), names=c("Monoculture","Mixed"))

```

R code for 2009 sediment and cattail biomass analysis at Delta Marsh

```

filePath="C:/Users/Jen/Documents/Cattail/Data/"
fileName=paste(filePath,"2009DeltaSed.csv",sep="")
DeltaData=read.table(fileName, header=TRUE, sep=",") #import data file

library(car)
library(ggplot2)

palette(gray(seq(.3,.9,len=25))) #change palette to grayscale

Date=(DeltaData$Date)
Transect=(DeltaData$Transect)

```

Location=(DeltaData\$Location)
GPSEasting=(DeltaData\$GPSEasting)
GPSNorthing=(DeltaData\$GPSNorthing)
Tangustifolia=(DeltaData\$Tangustifolia)
Txglauca=(DeltaData\$Txglauca)
Hybrid=(DeltaData\$Hybrid)
Hybrid<-as.factor(Hybrid)
Length=(DeltaData\$Length)
FloatingMat=(DeltaData\$FloatingMat)
WaterDepth=(DeltaData\$WaterDepth)
LitterDepth=(DeltaData\$LitterDepth)
LitterDepthSQRT=(DeltaData\$LitterDepthSQRT)
Density=(DeltaData\$Density)
Height=(DeltaData\$Height)
TotalBiomass=(DeltaData\$TotalBiomass)
TotalBiomassSQRT=(DeltaData\$TotalBiomassSQRT)
BiomassSLitter=(DeltaData\$BiomassSLitter)
BiomassSLitterSQRT=(DeltaData\$BiomassSLitterSQRT)
BiomassFLitter=(DeltaData\$BiomassFLitter)
TyphaSp=(DeltaData\$TyphaSp)
Conductivity=(DeltaData\$Conductivity)
ConductivityLn=(DeltaData\$ConductivityLn)
Texture=(DeltaData\$Texture)
TextureLn=(DeltaData\$TextureLn)
OrganicC=(DeltaData\$OrganicC)
TotalN=(DeltaData\$TotalN)
TotalNLn=(DeltaData\$TotalNLn)
Nitrate=(DeltaData\$Nitrate)
NitrateLn=(DeltaData\$NitrateLn)
OlsenP=(DeltaData\$OlsenP)
Location=(DeltaData\$Location)

```
Hybrid=(DeltaData$Hybrid)
```

```
summary(DeltaData)
boxplot(NFBiomass, horizontal=TRUE)
boxplot(NFBiomassLn, horizontal=TRUE)
boxplot(NFBiomassSQRT, horizontal=TRUE)
boxplot(FBiomass, horizontal=TRUE)
boxplot(FBiomassSQRT, horizontal=TRUE)
boxplot(TotalBiomass, horizontal=TRUE)
boxplot(TotalBiomassSQRT, horizontal=TRUE)
boxplot(FlowerPercent, horizontal=TRUE)
boxplot(FlowerPercentSQRT, horizontal=TRUE)
boxplot(LitterDepth, horizontal=TRUE)
boxplot(LitterDepthSQRT, horizontal=TRUE)

par(mar=c(4,1,1,1), mfrow=c(2,2), family="serif", cex=0.8)
boxplot(Nitrate, horizontal=TRUE,
       xlab=expression((a)~Nitrate-N~(mg~NO[3]-N~kg^-1)))
boxplot(NitrateLn, horizontal=TRUE,
       xlab=expression((b)~Ln~Nitrate-N~(Ln~mg~NO[3]-N~kg^-1)))
boxplot(Texture, horizontal=TRUE,
       xlab=expression("(c) Texture (%Clay)"))
boxplot(TextureLn, horizontal=TRUE,
       xlab=expression("(d) Ln Texture (Ln %Clay)"))
boxplot(Conductivity, horizontal=TRUE,
       xlab=expression((e)~Conductivity))
boxplot(ConductivityLn, horizontal=TRUE,
       xlab=expression((f)~Ln~Conductivity))

scatterplotMatrix(~Date + Texture + TotalN + Nitrate + OrganicC + OlsenP +
  Conductivity + Length,
```

```
data=DeltaData, diagonal=c("boxplot"), reg.line=FALSE,  
smooth=FALSE, transform=FALSE, cex.labels=0.75)
```

```
lmDateLength<-lm(Date~Length)  
summary(lmDateLength)  
anova(lmDateLength)
```

```
lmDateConductivity<-lm(Date~Conductivity)  
summary(lmDateConductivity)  
anova(lmDateConductivity)
```

```
lmDateTextureLn<-lm(Date~TextureLn)  
summary(lmDateTextureLn)  
anova(lmDateTextureLn)
```

```
lmDateTotalN<-lm(Date~TotalN)  
summary(lmDateTotalN)  
anova(lmDateTotalN)
```

```
lmDateNitrateLn<-lm(Date~NitrateLn)  
summary(lmDateNitrateLn)  
anova(lmDateNitrateLn)
```

```
lmDateOlsenP<-lm(Date~OlsenP)  
summary(lmDateOlsenP)  
anova(lmDateOlsenP)
```

```
lmDateOrganicC<-lm(Date~OrganicC)  
summary(lmDateOrganicC)  
anova(lmDateOrganicC)
```

```
lmLengthConductivity<-lm(Length~Conductivity)
summary(lmLengthConductivity)
anova(lmLengthConductivity)
```

```
lmLengthTextureLn<-lm(Length~TextureLn)
summary(lmLengthTextureLn)
anova(lmLengthTextureLn)
```

```
lmLengthTotalN<-lm(Length~TotalN)
summary(lmLengthTotalN)
anova(lmLengthTotalN)
```

```
lmLengthNitrateLn<-lm(Length~NitrateLn)
summary(lmLengthNitrateLn)
anova(lmLengthNitrateLn)
```

```
lmLengthOlsenP<-lm(Length~OlsenP)
summary(lmLengthOlsenP)
anova(lmLengthOlsenP)
```

```
lmLengthOrganicC<-lm(Length~OrganicC)
summary(lmLengthOrganicC)
anova(lmLengthOrganicC)
```

```
lmConductivityTextureLn<-lm(Conductivity~TextureLn)
summary(lmConductivityTextureLn)
anova(lmConductivityTextureLn)
```

```
lmConductivityTotalN<-lm(Conductivity~TotalN)
summary(lmConductivityTotalN)
anova(lmConductivityTotalN)
```

```
lmConductivityNitrateLn<-lm(Conductivity~NitrateLn)
```

```
summary(lmConductivityNitrateLn)
```

```
anova(lmConductivityNitrateLn)
```

```
lmConductivityOlsenP<-lm(Conductivity~OlsenP)
```

```
summary(lmConductivityOlsenP)
```

```
anova(lmConductivityOlsenP)
```

```
lmConductivityOrganicC<-lm(Conductivity~OrganicC)
```

```
summary(lmConductivityOrganicC)
```

```
anova(lmConductivityOrganicC)
```

```
lmTextureLnTotalN<-lm(TextureLn~TotalN)
```

```
summary(lmTextureLnTotalN)
```

```
anova(lmTextureLnTotalN)
```

```
lmTextureLnNitrateLn<-lm(TextureLn~NitrateLn)
```

```
summary(lmTextureLnNitrateLn)
```

```
anova(lmTextureLnNitrateLn)
```

```
lmTextureLnOlsenP<-lm(TextureLn~OlsenP)
```

```
summary(lmTextureLnOlsenP)
```

```
anova(lmTextureLnOlsenP)
```

```
lmTextureLnOrganicC<-lm(TextureLn~OrganicC)
```

```
summary(lmTextureLnOrganicC)
```

```
anova(lmTextureLnOrganicC)
```

```
lmTotalNNitrateLn<-lm(TotalN~NitrateLn)
```

```
summary(lmTotalNNitrateLn)
```

```
anova(lmTotalNNitrateLn)
```

```
lmTotalNOlsenP<-lm(TotalN~OlsenP)
```

```
summary(lmTotalNOlsenP)
```

```
anova(lmTotalNOlsenP)
```

```
lmTotalNOrganicC<-lm(TotalN~OrganicC)
```

```
summary(lmTotalNOrganicC)
```

```
anova(lmTotalNOrganicC)
```

```
lmNitrateLnOlsenP<-lm(NitrateLn~OlsenP)
```

```
summary(lmNitrateLnOlsenP)
```

```
anova(lmNitrateLnOlsenP)
```

```
lmNitrateLnOrganicC<-lm(NitrateLn~OrganicC)
```

```
summary(lmNitrateLnOrganicC)
```

```
anova(lmNitrateLnOrganicC)
```

```
lmOlsenPOrganicC<-lm(OlsenP~OrganicC)
```

```
summary(lmOlsenPOrganicC)
```

```
anova(lmOlsenPOrganicC)
```

```
ggplot(DeltaData, aes(y=TextureLn, x=TotalN)) +
  ylab(expression("Ln of sediment texture (Ln %Clay)")) +
  xlab(expression(Sediment~total-N~(mg~N~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_y_continuous(expand=c(0,0), limits=c(0,4)) +
  scale_x_continuous(expand=c(0,0), limits = c(1000,18000)) +
  geom_text(data=NULL, x=13000, y=3.8, label="y=3.08 - 1.16e-04x", colour="black",
            size=4) +
  theme(axis.line = element_line(colour = "black"),
```

```

axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(DeltaData, aes(y=NitrateLn, x=OlsenP)) +
ylab(expression(Ln~of~nitrate-N~(Ln~mg~NO[3]-N~kg^-1))) +
xlab(expression(Sediment~Olsen-P~(mg~P~kg^-1))) + geom_point() +
geom_smooth(method="lm", fullrange=TRUE) +
scale_y_continuous(expand=c(0,0), limits=c(0,5.6)) +
scale_x_continuous(expand = c(0,0), limits = c(0,40)) +
geom_text(data=NULL, x=8, y=5.3, label="y=1.74+0.059x", colour="black", size=4) +
theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

leveneTest(Length,Hybrid, center=mean)
LengthHybrid<-aov(Length~Hybrid)
summary(LengthHybrid)

leveneTest(Conductivity,Hybrid, center=mean)
ConductivityHybrid<-aov(Conductivity~Hybrid)
summary(ConductivityHybrid)

leveneTest(TextureLn,Hybrid, center=mean)
TextureLnHybrid<-aov(TextureLn~Hybrid)
summary(TextureLnHybrid)

```

```
leveneTest(TotalN,Hybrid, center=mean)
```

```
TotalNHybrid<-aov(TotalN~Hybrid)
```

```
summary(TotalNHybrid)
```

```
leveneTest(NitrateLn,Hybrid, center=mean)
```

```
NitrateLnHybrid<-aov(NitrateLn~Hybrid)
```

```
summary(NitrateLnHybrid)
```

```
leveneTest(OlsenP,Hybrid, center=mean)
```

```
OlsenPHybrid<-aov(OlsenP~Hybrid)
```

```
summary(OlsenPHybrid)
```

```
leveneTest(OrganicC,Hybrid, center=mean)
```

```
OrganicCHybrid<-aov(OrganicC~Hybrid)
```

```
summary(OrganicCHybrid)
```

```
lmTotalBiomassSQRTLength<-lm(TotalBiomassSQRT~Length)
```

```
summary(lmTotalBiomassSQRTLength)
```

```
anova(lmTotalBiomassSQRTLength)
```

```
lmTotalBiomassSQRTConductivity<-lm(TotalBiomassSQRT~Conductivity)
```

```
summary(lmTotalBiomassSQRTConductivity)
```

```
anova(lmTotalBiomassSQRTConductivity)
```

```
lmTotalBiomassSQRTTextureLn<-lm(TotalBiomassSQRT~TextureLn)
```

```
summary(lmTotalBiomassSQRTTextureLn)
```

```
anova(lmTotalBiomassSQRTTextureLn)
```

```
lmTotalBiomassSQRTTotalN<-lm(TotalBiomassSQRT~TotalN)
```

```
summary(lmTotalBiomassSQRTTotalN)
```

```
anova(lmTotalBiomassSQRTTotalN)
```

```
lmTotalBiomassSQRTNitrateLn<-lm(TotalBiomassSQRT~NitrateLn)  
summary(lmTotalBiomassSQRTNitrateLn)  
anova(lmTotalBiomassSQRTNitrateLn)
```

```
lmTotalBiomassSQRTOlsenP<-lm(TotalBiomassSQRT~OlsenP)  
summary(lmTotalBiomassSQRTOlsenP)  
anova(lmTotalBiomassSQRTOlsenP)
```

```
lmTotalBiomassSQORTOrganicC<-lm(TotalBiomassSQRT~OrganicC)  
summary(lmTotalBiomassSQORTOrganicC)  
anova(lmTotalBiomassSQORTOrganicC)
```

```
lmBiomassFLitterLength<-lm(BiomassFLitter~Length)  
summary(lmBiomassFLitterLength)  
anova(lmBiomassFLitterLength)
```

```
lmBiomassFLitterConductivity<-lm(BiomassFLitter~Conductivity)  
summary(lmBiomassFLitterConductivity)  
anova(lmBiomassFLitterConductivity)
```

```
lmBiomassFLitterTextureLn<-lm(BiomassFLitter~TextureLn)  
summary(lmBiomassFLitterTextureLn)  
anova(lmBiomassFLitterTextureLn)
```

```
lmBiomassFLitterTotalN<-lm(BiomassFLitter~TotalN)  
summary(lmBiomassFLitterTotalN)  
anova(lmBiomassFLitterTotalN)
```

```
lmBiomassFLitterNitrateLn<-lm(BiomassFLitter~NitrateLn)
```

```
summary(lmBiomassFLitterNitrateLn)
```

```
anova(lmBiomassFLitterNitrateLn)
```

```
lmBiomassFLitterOlsenP<-lm(BiomassFLitter~OlsenP)
```

```
summary(lmBiomassFLitterOlsenP)
```

```
anova(lmBiomassFLitterOlsenP)
```

```
lmBiomassFLitterOrganicC<-lm(BiomassFLitter~OrganicC)
```

```
summary(lmBiomassFLitterOrganicC)
```

```
anova(lmBiomassFLitterOrganicC)
```

```
lmBiomassSLitterSQRTLength<-lm(BiomassSLitterSQRT~Length)
```

```
summary(lmBiomassSLitterSQRTLength)
```

```
anova(lmBiomassSLitterSQRTLength)
```

```
lmBiomassSLitterSQRTConductivity<-lm(BiomassSLitterSQRT~Conductivity)
```

```
summary(lmBiomassSLitterSQRTConductivity)
```

```
anova(lmBiomassSLitterSQRTConductivity)
```

```
lmBiomassSLitterSQRTTextureLn<-lm(BiomassSLitterSQRT~TextureLn)
```

```
summary(lmBiomassSLitterSQRTTextureLn)
```

```
anova(lmBiomassSLitterSQRTTextureLn)
```

```
lmBiomassSLitterSQRTTotalN<-lm(BiomassSLitterSQRT~TotalN)
```

```
summary(lmBiomassSLitterSQRTTotalN)
```

```
anova(lmBiomassSLitterSQRTTotalN)
```

```
lmBiomassSLitterSQRTNitrateLn<-lm(BiomassSLitterSQRT~NitrateLn)
```

```
summary(lmBiomassSLitterSQRTNitrateLn)
```

```
anova(lmBiomassSLitterSQRTNitrateLn)
```

```
lmBiomassSLitterSQRTOlsenP<-lm(BiomassSLitterSQRT~OlsenP)
summary(lmBiomassSLitterSQRTOlsenP)
anova(lmBiomassSLitterSQRTOlsenP)
```

```
lmBiomassSLitterSQORTOrganicC<-lm(BiomassSLitterSQRT~OrganicC)
summary(lmBiomassSLitterSQORTOrganicC)
anova(lmBiomassSLitterSQORTOrganicC)
```

```
lmHeightLength<-lm(Height~Length)
summary(lmHeightLength)
anova(lmHeightLength)
```

```
lmHeightConductivity<-lm(Height~Conductivity)
summary(lmHeightConductivity)
anova(lmHeightConductivity)
```

```
lmHeightTextureLn<-lm(Height~TextureLn)
summary(lmHeightTextureLn)
anova(lmHeightTextureLn)
```

```
lmHeightTotalN<-lm(Height~TotalN)
summary(lmHeightTotalN)
anova(lmHeightTotalN)
```

```
lmHeightNitrateLn<-lm(Height~NitrateLn)
summary(lmHeightNitrateLn)
anova(lmHeightNitrateLn)
```

```
lmHeightOlsenP<-lm(Height~OlsenP)
summary(lmHeightOlsenP)
anova(lmHeightOlsenP)
```

```

lmHeightOrganicC<-lm(Height~OrganicC)
summary(lmHeightOrganicC)
anova(lmHeightOrganicC)

ggplot(DeltaData, aes(y=BiomassSLitterSQRT, x=NitrateLn)) +
  ylab(expression(SQRT~standing~litter~biomass~(sqrt("g m"^-2)))) +
  xlab(expression(Ln~of~nitrate-N~(Ln~mg~NO[3]-N~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_y_continuous(expand = c(0,0), limits = c(-2.5,55)) +
  scale_x_continuous(expand=c(0,0), limits=c(0,4.5)) +
  geom_text(data=NULL, x=3, y=50, label="y=36.7-6.19x", colour="black", size=4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(DeltaData, aes(y=BiomassSLitterSQRT, x=OlsenP)) +
  ylab(expression(SQRT~standing~litter~biomass~(sqrt("g m"^-2)))) +
  xlab(expression(Sediment~Olsen-P~(mg~P~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_y_continuous(expand = c(0,0), limits = c(-2.5,40)) +
  scale_x_continuous(expand = c(0,0), limits = c(0,40)) +
  geom_text(data=NULL, x=30, y=38, label="y=30.6-0.62x", colour="black", size=4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),

```

```
panel.background = element_rect(colour="black", fill="NA"))
```

**R code for analyzing the environment in 2011 pothole and ditch
marshes in southwestern Manitoba and southeastern
Saskatchewan**

```
filePath="C:/Users/Jen/Documents/Cattail/Data/"
fileName=paste(filePath,"2011CattailAll.csv",sep="")
PotholeData=read.table(fileName, header=TRUE, sep=",") #import data file

library(car)
library(glmulti)
library(Hotelling)
library(ggplot2)
summary(PotholeData) #summarize data, calculate means, quantiles

palette(gray(seq(.2,.9,len=25))) #change palette to grayscale

Txglauca=(PotholeData$Txglauca)
Tlatifolia=(PotholeData$Tlatifolia)
TxglaucaP=(PotholeData$TxglaucaP)
Texture=(PotholeData$Texture)
OrganicC=(PotholeData$OrganicC)
OrganicCLn=(PotholeData$OrganicCLn)
TotalN=(PotholeData$TotalN)
TotalNLn=(PotholeData$TotalNLn)
Ammonium=(PotholeData$Ammonium)
AmmoniumLn=(PotholeData$AmmoniumLn)
Nitrate=(PotholeData$Nitrate)
NitrateSQRT=(PotholeData$NitrateSQRT)
```

```

OlsenP=(PotholeData$OlsenP)
OlsenPSQRT=(PotholeData$OlsenPSQRT)
Conductivity=(PotholeData$Conductivity)
ConductivityLn=(PotholeData$ConductivityLn)
pH=(PotholeData$pH)
DN=(PotholeData$DN)
DNLn=(PotholeData$DNLn)
DOC=(PotholeData$DOC)
DOCLn=(PotholeData$DOCLn)
GPSNorthing=(PotholeData$GPSNorthing)
GPSEasting=(PotholeData$GPSEasting)
Date=(PotholeData$Date)
Length=(PotholeData$Length)
LengthLn=(PotholeData$LengthLn)
LandUse=(PotholeData$LandUse)
LandUseC=(PotholeData$LandUseC)
Type=(PotholeData>Type)
Litter=(PotholeData$Litter)
LitterSQRT=(PotholeData$LitterSQRT)

```

```

par(fig=c(0,1,0,1), mar=c(4, 1, 1, 1))
dotchart(TxglaucaP,
lcol=NA, xlab="Proportion of hybrid cattail")
par(fig=c(0,1,0,1),mar=c(4, 4, 1, 1))
stripchart(TxglaucaP~Type, pch=c(16,1), method="stack", offset=0.5,
xaxt="n", ylab="Marsh type", ylim=c(0.8,2.7),
xlab="Proportion of hybrid cattail", cex=1)
axis(1, at=c("0", "0.17", "0.33", "0.50", "0.67", "0.83", "1"), labels=c("0", "0.17", "0.33",
"0.50", "0.67", "0.83", "1"))

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))

```

```
stripchart(Texture~TxglaucaP, pch=c(16,1),
method="stack", offset=0.5,
vertical=FALSE,
xlim=c(0,45), ylim=c(1, 8),
ylab="Proportion of hybrid cattail",
xlab="Sediment texture (% Clay)")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))

boxplot(Texture~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab="Sediment texture (% Clay)")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(TextureLn~TxglaucaP, pch=c(16,1),
method="stack", offset=0.5,
vertical=FALSE,
xlim=c(0,4),ylim=c(1, 8),
ylab="Proportion of hybrid cattail",
xlab="Sediment texture (Ln % Clay)")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))

boxplot(TextureLn~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab="Sediment texture (Ln % Clay)")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(OrganicC~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(10000,200000),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~organic-C~(mg~organic-C~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))

boxplot(OrganicC~TxglaucaP, horizontal=TRUE,
```

```

ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~organic-C~(mg~organic-C~kg^-1)))

par(fig=c(0,1,0,1))
qqnorm(OrganicC, main=NA, sub="Normal Q-Q Plot for Sediment Organic-C")
qqline(OrganicC)

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(OrganicCLn~Txglaucap, pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(9,13),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~organic-C~(Ln~mg~organic-C~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(OrganicCLn~Txglaucap, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~organic-C~(Ln~mg~organic-C~kg^-1)))

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(TotalN~Txglaucap, pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(1000,17500),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~total-N~(mg~N~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(TotalN~Txglaucap, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~total-N~(mg~N~kg^-1)))

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(TotalNLn~Txglaucap, pch=c(16,1),

```

```

method="stack", offset=0.5, vertical=FALSE,
xlim=c(7,10),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~total-N~(Ln~mg~N~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(TotalNLn~Txglaucap, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~total-N~(Ln~mg~N~kg^-1)))

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(Ammonium~Txglaucap,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(2,50),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~ammonium~(mg~NH[4]-N~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(Ammonium~Txglaucap, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~ammonium~(mg~NH[4]-N~kg^-1)))

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(AmmoniumLn~Txglaucap,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(0.5,4),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~ammonium~(Ln~mg~NH[4]-N~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(AmmoniumLn~Txglaucap, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~ammonium~(Ln~mg~NH[4]-N~kg^-1)))

```

```

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(Nitrate~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(0,5),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~nitrate~(mg~NO[3]-N~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(Nitrate~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~nitrate~(mg~NO[3]-N~kg^-1)))

```

```

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(NitrateLn~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(-4,2),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~nitrate~(Ln~mg~NO[3]-N~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(NitrateLn~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~nitrate~(Ln~mg~NO[3]-N~kg^-1)))

```

```

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(NitrateSQRT~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(0,2.5),
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~nitrate~(SQRT~mg~NO[3]-N~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(NitrateSQRT~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",

```

```

xlab=expression(Sediment~nitrate~(SQRT~mg~NO[3]-N~kg^-1)))

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(OlsenP~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(0,40), ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~Olsen-P~(mg~P~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(OlsenP~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~Olsen-P~(mg~P~kg^-1)))

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(OlsenPSQRT~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(0,6.5), ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~Olsen-P~(SQRT~mg~P~kg^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(OlsenPSQRT~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab=expression(Sediment~Olsen-P~(SQRT~mg~P~kg^-1)))
boxplot(OlsenP)
boxplot(OlsenPSQRT)

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(Conductivity~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(300,3500), ylab="Proportion of hybrid cattail",
xlab=expression(Water~conductivity~(mu*S~cm^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(Conductivity~TxglaucaP, horizontal=TRUE,

```

```

ylab="Proportion of hybrid cattail",
xlab=expression(Water~conductivity~(mu*S~cm^-1)))

par(fig=c(0,1,0,1))
qqnorm(Conductivity, main=NA, sub="Normal Q-Q Plot for Water Conductivity",
       ylab=expression((mu*S~cm^-1)))
qqline(Conductivity)

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(ConductivityLn~TxglaucaP,pch=c(16,1),
           method="stack", offset=0.5, vertical=FALSE,
           xlim=c(5,8.5),
           ylab="Proportion of hybrid cattail",
           xlab=expression(Water~conductivity~(Ln~mu*S~cm^-1)))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(ConductivityLn~TxglaucaP, horizontal=TRUE,
        ylab="Proportion of hybrid cattail",
        xlab=expression(Water~conductivity~(Ln~mu*S~cm^-1)))
boxplot(Conductivity)
boxplot(ConductivityLn)

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(pH~TxglaucaP,pch=c(16,1),
           method="stack", offset=0.5, vertical=FALSE,
           xlim=c(6.5,9.5),
           ylab="Proportion of hybrid cattail",
           xlab="Water pH")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(pH~TxglaucaP, horizontal=TRUE,
        ylab="Proportion of hybrid cattail",
        xlab="Water pH")

```

```

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(DN~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE, xlim=c(0,100),
xlab=expression(Water~dissolved-N~(mg~DN~L^-1)),
ylab="Proportion of hybrid cattail")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(DN~TxglaucaP, horizontal=TRUE,
xlab=expression(Water~dissolved-N~(mg~DN~L^-1)),
ylab="Proportion of hybrid cattail")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(DNLn~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(0,5),
xlab=expression(Water~dissolved-N~(Ln~mg~DN~L^-1)),
ylab="Proportion of hybrid cattail")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(DNLn~TxglaucaP, horizontal=TRUE,
xlab=expression(Water~dissolved-N~(Ln~mg~DN~L^-1)),
ylab="Proportion of hybrid cattail")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(DOC~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(30,260),
xlab=expression(Water~DOC~(mg~DOC~L^-1)),
ylab="Proportion of hybrid cattail")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(DOC~TxglaucaP, horizontal=TRUE,
xlab=expression(Water~DOC~(mg~DOC~L^-1)),

```

```

ylab="Proportion of hybrid cattail")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(DOCLn~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(3,6),
xlab=expression(Water~DOC~(Ln~mg~DOC~L^-1)),
ylab="Proportion of hybrid cattail")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(DOCLn~TxglaucaP, horizontal=TRUE,
xlab=expression(Water~DOC~(Ln~mg~DOC~L^-1)),
ylab="Proportion of hybrid cattail")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(GPSNorthing~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(5400000,5700000),
ylab="Proportion of hybrid cattail",
xlab="GPS Northing UTM Zone 14N, NAD 1983,
Transverse Mercator")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(GPSNorthing~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab="GPS Northing UTM Zone 14N, NAD 1983,
Transverse Mercator")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(GPSEasting~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(300000,700000),
ylab="Proportion of hybrid cattail",

```

```

xlab="GPS Easting UTM Zone 14N, NAD 1983,
Transverse Mercator")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(GPSEasting~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab="GPS Easting UTM Zone 14N, NAD 1983,
Transverse Mercator")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(Date~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(40720,40790),
ylab="Proportion of hybrid cattail",
xaxt="n", xlab="2011 Sampling Date")
axis(1, at=c("40725", "40756", "40786"),
labels=c("01 Jul", "01 Aug", "31 Aug"))
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(Date~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xaxt="n", xlab="2011 Sampling Date")
axis(1, at=c("40725", "40756", "40786"),
labels=c("01 Jul", "01 Aug", "31 Aug"))

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(Length~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(0,55),
ylab="Proportion of hybrid cattail",
xlab="Transect length (m)")
par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(Length~TxglaucaP, horizontal=TRUE,

```

```
ylab="Proportion of hybrid cattail",
xlab="Transect length (m)")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
stripchart(LengthLn~TxglaucaP,pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
xlim=c(0.5,4),
ylab="Proportion of hybrid cattail",
xlab="Transect length (Ln~m)")

par(fig=c(0,1,0,1), mar=c(4, 4, 1, 1))
boxplot(LengthLn~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab="Transect Length (Ln~m)")

par(fig=c(0,1,0,1), mar=c(4,4,1,1))
stripchart(TxglaucaP~LandUseC, pch=c(16,1),
method="stack", offset=0.5, vertical=FALSE,
ylim=c(1.0,5),
ylab="Surrounding land use",
xlab="Proportion of hybrid cattail")

par(fig=c(0,1,0,1), mar=c(6,4,1,1))
stripchart(TxglaucaP~Type, pch=c(16,1),
method="stack", offset=0.5,
ylim=c(0.5,3),
ylab="Marsh type",
xlab="Proportion of hybrid cattail")

par(fig=c(0,1,0,1), mar=c(6,4,1,1))
stripchart(Litter~TxglaucaP, pch=c(16,1),
method="stack", offset=0.5,
```

```

ylim=c(1,9.5),
ylab="Proportion of hybrid cattail",
xlab="Average litter depth (cm)"
par(fig=c(0,1,0,1), mar=c(6,4,1,1))
boxplot(Litter~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab="Average litter depth (cm)")
qqnorm(Litter)

par(fig=c(0,1,0,1), mar=c(6,4,1,1))
stripchart(LitterSQRT~TxglaucaP, pch=c(16,1),
method="stack", offset=0.5,
ylim=c(1,9.5),
ylab="Proportion of hybrid cattail",
xlab="Average litter depth (SQRT~cm)")
par(fig=c(0,1,0,1), mar=c(6,4,1,1))
boxplot(LitterSQRT~TxglaucaP, horizontal=TRUE,
ylab="Proportion of hybrid cattail",
xlab="Average litter depth (SQRT~cm)")
qqnorm(LitterSQRT)

par(fig=c(0,1,0,1), mar=c(4, 5, 1, 1))
plot(OlsenP, GPSNorthing,
xlim=c(0,40), ylab="GPS Northing
(UTM Zone 14N, NAD 1983, Transverse Mercator)",
xlab=expression(Sediment~Olsen-P~(mg~P~kg^-1)))

par(fig=c(0,1,0,1), mar=c(4, 5, 1, 1))
plot(DOC, GPSNorthing,
ylab="GPS Northing
(UTM Zone 14N, NAD 1983, Transverse Mercator)",

```

```

xlab=expression(Water~DOC~(mg~DOC~L^-1)))

par(fig=c(0,1,0,1), mar=c(4, 3, 3, 3))
cdplot(OlsenP,LandUseC,ylab=NA,
xlab=expression((mg~P~L^-1)))

par(fig=c(0,1,0,1), mar=c(4, 3, 3, 3))
cdplot(TotalNLn,LandUseC, ylab=NA,
xlab=expression((Ln~mg~N~L^-1)))

par(fig=c(0,1,0,1), mar=c(4, 3, 3, 3))
cdplot(Ammonium,LandUseC, ylab=NA,
xlab=expression((mg~NH[4]-N~kg^-1)))

par(mfrow=c(6,2))
boxplot(TotalN, horizontal=TRUE,
xlab=expression((a)~Total-N~(mg~N~kg^-1)))
boxplot(TotalNLn, horizontal=TRUE,
xlab=expression((b)~Ln~total-N~(Ln~mg~N~kg^-1)))
boxplot(Ammonium, horizontal=TRUE,
xlab=expression((c)~Ammonium~(mg~NH[4]-N~kg^-1)))
boxplot(AmmoniumLn, horizontal=TRUE,
xlab=expression((d)~Ln~ammonium~(Ln~mg~NH[4]-N~kg^-1)))
boxplot(DN, horizontal=TRUE,
xlab=expression((e)~Dissolved-N~(mg~DN~L^-1)))
boxplot(DNLn, horizontal=TRUE,
xlab=expression((f)~Ln~dissolved-N~(Ln~mg~DN~L^-1)))
boxplot(DOC, horizontal=TRUE,
xlab=expression((g)~DOC~(mg~DOC~L^-1)))
boxplot(DOCLn, horizontal=TRUE,
xlab=expression((h)~Ln~DOC~(Ln~mg~DOC~L^-1)))

```

```

boxplot(Conductivity, horizontal=TRUE,
        xlab=expression((i)~Conductivity~(mu*S~cm^-1)))
boxplot(ConductivityLn, horizontal=TRUE,
        xlab=expression((j)~Ln~conductivity~(Ln~mu*S~cm^-1)))
boxplot(Length, horizontal=TRUE,
        xlab="(k) Transect length (m)")
boxplot(LengthLn, horizontal=TRUE,
        xlab="(l) Ln Transect Length (Ln m)")

```

```

Hotelltest1<-hotelling.test(Texture + TotalNLn + AmmoniumLn + Nitrate +
    OrganicC + OlsenP + ConductivityLn + DNLn +
    DOCLn + pH + Date + GPSNorthing + GPSEasting +
    LengthLn + Litter~Type, data=PotholeData)

```

Hotelltest1

p-value > 0.05 pothole and ditch environments not significantly diff.

```

Hotelltest2<-hotelling.test(Texture + TotalNLn + AmmoniumLn + Nitrate +
    OrganicC + OlsenP + ConductivityLn + DNLn +
    DOCLn + pH + Date + GPSNorthing + GPSEasting +
    LengthLn~Type, data=PotholeData)

```

Hotelltest2

p-value > 0.05 pothole and ditch environments not significantly diff.

even when litter is removed (which did not meet normal distr. requirements)

```

Hotelltest3<-hotelling.test(Texture + TotalNLn + AmmoniumLn + Nitrate +
    OrganicC + OlsenP + ConductivityLn + DNLn +
    DOCLn + pH ~ Type, data=PotholeData)

```

Hotelltest3

```

scatterplotMatrix(~TxglaucaP + Texture + OrganicC + TotalNLn +
    AmmoniumLn + Nitrate + OlsenP + Conductivity + DNLn +

```

```
DOCLn + pH + Date + GPSNorthing + GPSEasting + LengthLn +  
Litter, data = PotholeData, diag="boxplot", reg.line=FALSE,  
smooth=FALSE, transform=FALSE, cex.labels=1.5)
```

```
lmDateGPSEasting<-lm(GPSEasting~Date)  
summary(lmDateGPSEasting)  
anova(lmDateGPSEasting)
```

```
lmDateGPSNorthing<-lm(GPSNorthing~Date)  
summary(lmDateGPSNorthing)  
anova(lmDateGPSNorthing)
```

```
lmDateLengthLn<-lm(LengthLn~Date)  
summary(lmDateLengthLn)  
anova(lmDateLengthLn)
```

```
lmDateLitter<-lm(Litter~Date)  
summary(lmDateLitter)  
anova(lmDateLitter)
```

```
lmDateConductivityLn<-lm(ConductivityLn~Date)  
summary(lmDateConductivityLn)  
anova(lmDateConductivityLn)
```

```
lmDatepH<-lm(pH~Date)  
summary(lmDatepH)  
anova(lmDatepH)
```

```
lmDateDNLn<-lm(DNLn~Date)  
summary(lmDateDNLn)  
anova(lmDateDNLn)
```

```
lmDateDOCLn<-lm(DOCLn~Date)
```

```
summary(lmDateDOCLn)
```

```
anova(lmDateDOCLn)
```

```
lmDateTexture<-lm(Texture~Date)
```

```
summary(lmDateTexture)
```

```
anova(lmDateTexture)
```

```
lmDateOlsenP<-lm(OlsenP~Date)
```

```
summary(lmDateOlsenP)
```

```
anova(lmDateOlsenP)
```

```
lmDateTotalNLn<-lm(TotalNLn~Date)
```

```
summary(lmDateTotalNLn)
```

```
anova(lmDateTotalNLn)
```

```
lmDateAmmoniumLn<-lm(AmmoniumLn~Date)
```

```
summary(lmDateAmmoniumLn)
```

```
anova(lmDateAmmoniumLn)
```

```
lmDateNitrate<-lm(Nitrate~Date)
```

```
summary(lmDateNitrate)
```

```
anova(lmDateNitrate)
```

```
lmDateOrganicC<-lm(OrganicC~Date)
```

```
summary(lmDateOrganicC)
```

```
anova(lmDateOrganicC)
```

```
lmGPSEastingGPSNorthing<-lm(GPSNorthing~GPSEasting)
```

```
summary(lmGPSEastingGPSNorthing)
```

```
anova(lmGPSEastingGPSNorthing)
```

```
lmGPSEastingLengthLn<-lm(LengthLn~GPSEasting)  
summary(lmGPSEastingLengthLn)  
anova(lmGPSEastingLengthLn)
```

```
lmGPSEastingLitter<-lm(Litter~GPSEasting)  
summary(lmGPSEastingLitter)  
anova(lmGPSEastingLitter)
```

```
lmGPSEastingConductivityLn<-lm(ConductivityLn~GPSEasting)  
summary(lmGPSEastingConductivityLn)  
anova(lmGPSEastingConductivityLn)
```

```
lmGPSEastingpH<-lm(pH~GPSEasting)  
summary(lmGPSEastingpH)  
anova(lmGPSEastingpH)
```

```
lmGPSEastingDNLn<-lm(DNLn~GPSEasting)  
summary(lmGPSEastingDNLn)  
anova(lmGPSEastingDNLn)
```

```
lmGPSEastingDOCLn<-lm(DOCLn~GPSEasting)  
summary(lmGPSEastingDOCLn)  
anova(lmGPSEastingDOCLn)
```

```
lmGPSEastingTexture<-lm(Texture~GPSEasting)  
summary(lmGPSEastingTexture)  
anova(lmGPSEastingTexture)
```

```
lmGPSEastingOlsenP<-lm(OlsenP~GPSEasting)
```

```
summary(lmGPSEastingOlsenP)
```

```
anova(lmGPSEastingOlsenP)
```

```
lmGPSEastingTotalNLn<-lm(TotalNLn~GPSEasting)
```

```
summary(lmGPSEastingTotalNLn)
```

```
anova(lmGPSEastingTotalNLn)
```

```
lmGPSEastingAmmoniumLn<-lm(AmmoniumLn~GPSEasting)
```

```
summary(lmGPSEastingAmmoniumLn)
```

```
anova(lmGPSEastingAmmoniumLn)
```

```
lmGPSEastingNitrate<-lm(Nitrate~GPSEasting)
```

```
summary(lmGPSEastingNitrate)
```

```
anova(lmGPSEastingNitrate)
```

```
lmGPSEastingOrganicC<-lm(OrganicC~GPSEasting)
```

```
summary(lmGPSEastingOrganicC)
```

```
anova(lmGPSEastingOrganicC)
```

```
lmGPSNorthingLengthLn<-lm(LengthLn~GPSNorthing)
```

```
summary(lmGPSNorthingLengthLn)
```

```
anova(lmGPSNorthingLengthLn)
```

```
lmGPSNorthingLitter<-lm(Litter~GPSNorthing)
```

```
summary(lmGPSNorthingLitter)
```

```
anova(lmGPSNorthingLitter)
```

```
lmGPSNorthingConductivityLn<-lm(ConductivityLn~GPSNorthing)
```

```
summary(lmGPSNorthingConductivityLn)
```

```
anova(lmGPSNorthingConductivityLn)
```

```
lmGPSNorthingpH<-lm(pH~GPSNorthing)
summary(lmGPSNorthingpH)
anova(lmGPSNorthingpH)
```

```
lmGPSNorthingDNLn<-lm(DNLn~GPSNorthing)
summary(lmGPSNorthingDNLn)
anova(lmGPSNorthingDNLn)
```

```
lmGPSNorthingDOCLn<-lm(DOCLn~GPSNorthing)
summary(lmGPSNorthingDOCLn)
anova(lmGPSNorthingDOCLn)
```

```
lmGPSNorthingTexture<-lm(Texture~GPSNorthing)
summary(lmGPSNorthingTexture)
anova(lmGPSNorthingTexture)
```

```
lmGPSNorthingOlsenP<-lm(OlsenP~GPSNorthing)
summary(lmGPSNorthingOlsenP)
anova(lmGPSNorthingOlsenP)
```

```
lmGPSNorthingTotalNLn<-lm(TotalNLn~GPSNorthing)
summary(lmGPSNorthingTotalNLn)
anova(lmGPSNorthingTotalNLn)
```

```
lmGPSNorthingAmmoniumLn<-lm(AmmoniumLn~GPSNorthing)
summary(lmGPSNorthingAmmoniumLn)
anova(lmGPSNorthingAmmoniumLn)
```

```
lmGPSNorthingNitrate<-lm(Nitrate~GPSNorthing)
summary(lmGPSNorthingNitrate)
anova(lmGPSNorthingNitrate)
```

```
lmGPSNorthingOrganicC<-lm(OrganicC~GPSNorthing)
```

```
summary(lmGPSNorthingOrganicC)
```

```
anova(lmGPSNorthingOrganicC)
```

```
lmLengthLnLitter<-lm(Litter~LengthLn)
```

```
summary(lmLengthLnLitter)
```

```
anova(lmLengthLnLitter)
```

```
lmLengthLnConductivityLn<-lm(ConductivityLn~LengthLn)
```

```
summary(lmLengthLnConductivityLn)
```

```
anova(lmLengthLnConductivityLn)
```

```
lmLengthLnnpH<-lm(pH~LengthLn)
```

```
summary(lmLengthLnnpH)
```

```
anova(lmLengthLnnpH)
```

```
lmLengthLnDNLn<-lm(DNLn~LengthLn)
```

```
summary(lmLengthLnDNLn)
```

```
anova(lmLengthLnDNLn)
```

```
lmLengthLnDOCLn<-lm(DOCLn~LengthLn)
```

```
summary(lmLengthLnDOCLn)
```

```
anova(lmLengthLnDOCLn)
```

```
lmLengthLnTexture<-lm(Texture~LengthLn)
```

```
summary(lmLengthLnTexture)
```

```
anova(lmLengthLnTexture)
```

```
lmLengthLnOlsenP<-lm(OlsenP~LengthLn)
```

```
summary(lmLengthLnOlsenP)
```

```
anova(lmLengthLnOlsenP)
```

```
lmLengthLnTotalNLn<-lm(TotalNLn~LengthLn)
summary(lmLengthLnTotalNLn)
anova(lmLengthLnTotalNLn)
```

```
lmLengthLnAmmoniumLn<-lm(AmmoniumLn~LengthLn)
summary(lmLengthLnAmmoniumLn)
anova(lmLengthLnAmmoniumLn)
```

```
lmLengthLnNitrate<-lm(Nitrate~LengthLn)
summary(lmLengthLnNitrate)
anova(lmLengthLnNitrate)
```

```
lmLengthLnOrganicC<-lm(OrganicC~LengthLn)
summary(lmLengthLnOrganicC)
anova(lmLengthLnOrganicC)
```

```
lmLitterConductivityLn<-lm(ConductivityLn~Litter)
summary(lmLitterConductivityLn)
anova(lmLitterConductivityLn)
```

```
lmLitterpH<-lm(pH~Litter)
summary(lmLitterpH)
anova(lmLitterpH)
```

```
lmLitterDNLn<-lm(DNLn~Litter)
summary(lmLitterDNLn)
anova(lmLitterDNLn)
```

```
lmLitterDOCLn<-lm(DOCLn~Litter)
```

```
summary(lmLitterDOCLn)
```

```
anova(lmLitterDOCLn)
```

```
lmLitterTexture<-lm(Texture~Litter)
```

```
summary(lmLitterTexture)
```

```
anova(lmLitterTexture)
```

```
lmLitterOlsenP<-lm(OlsenP~Litter)
```

```
summary(lmLitterOlsenP)
```

```
anova(lmLitterOlsenP)
```

```
lmLitterTotalNLn<-lm(TotalNLn~Litter)
```

```
summary(lmLitterTotalNLn)
```

```
anova(lmLitterTotalNLn)
```

```
lmLitterAmmoniumLn<-lm(AmmoniumLn~Litter)
```

```
summary(lmLitterAmmoniumLn)
```

```
anova(lmLitterAmmoniumLn)
```

```
lmLitterNitrate<-lm(Nitrate~Litter)
```

```
summary(lmLitterNitrate)
```

```
anova(lmLitterNitrate)
```

```
lmLitterOrganicC<-lm(OrganicC~Litter)
```

```
summary(lmLitterOrganicC)
```

```
anova(lmLitterOrganicC)
```

```
lmConductivityLnpH<-lm(pH~ConductivityLn)
```

```
summary(lmConductivityLnpH)
```

```
anova(lmConductivityLnpH)
```

```
lmConductivityLnDNLn<-lm(DNLn~ConductivityLn)
```

```
summary(lmConductivityLnDNLn)
```

```
anova(lmConductivityLnDNLn)
```

```
lmConductivityLnDOCLn<-lm(DOCLn~ConductivityLn)
```

```
summary(lmConductivityLnDOCLn)
```

```
anova(lmConductivityLnDOCLn)
```

```
lmConductivityLnTexture<-lm(Texture~ConductivityLn)
```

```
summary(lmConductivityLnTexture)
```

```
anova(lmConductivityLnTexture)
```

```
lmConductivityLnOlsenP<-lm(OlsenP~ConductivityLn)
```

```
summary(lmConductivityLnOlsenP)
```

```
anova(lmConductivityLnOlsenP)
```

```
lmConductivityLnTotalNLn<-lm(TotalNLn~ConductivityLn)
```

```
summary(lmConductivityLnTotalNLn)
```

```
anova(lmConductivityLnTotalNLn)
```

```
lmConductivityLnAmmoniumLn<-lm(AmmoniumLn~ConductivityLn)
```

```
summary(lmConductivityLnAmmoniumLn)
```

```
anova(lmConductivityLnAmmoniumLn)
```

```
lmConductivityLnNitrate<-lm(Nitrate~ConductivityLn)
```

```
summary(lmConductivityLnNitrate)
```

```
anova(lmConductivityLnNitrate)
```

```
lmConductivityLnOrganicC<-lm(OrganicC~ConductivityLn)
```

```
summary(lmConductivityLnOrganicC)
```

```
anova(lmConductivityLnOrganicC)
```

```
lmpHDLN<-lm(DLN~pH)
```

```
summary(lmpHDLN)
```

```
anova(lmpHDLN)
```

```
lmpHDOCLN<-lm(DOCLN~pH)
```

```
summary(lmpHDOCLN)
```

```
anova(lmpHDOCLN)
```

```
lmpHTexture<-lm(Texture~pH)
```

```
summary(lmpHTexture)
```

```
anova(lmpHTexture)
```

```
lmpHOlsenP<-lm(OlsenP~pH)
```

```
summary(lmpHOlsenP)
```

```
anova(lmpHOlsenP)
```

```
lmpHTotalNLN<-lm(TotalNLN~pH)
```

```
summary(lmpHTotalNLN)
```

```
anova(lmpHTotalNLN)
```

```
lmpHAMmoniumLN<-lm(AmmoniumLN~pH)
```

```
summary(lmpHAMmoniumLN)
```

```
anova(lmpHAMmoniumLN)
```

```
lmpHNitrate<-lm(Nitrate~pH)
```

```
summary(lmpHNitrate)
```

```
anova(lmpHNitrate)
```

```
lmpHOrganicC<-lm(OrganicC~pH)
```

```
summary(lmpHOrganicC)
```

```
anova(lmPHOrganicC)
```

```
lmDNLnDOCLn<-lm(DOCLn~DNLn)  
summary(lmDNLnDOCLn)  
anova(lmDNLnDOCLn)
```

```
lmDNLnTexture<-lm(Texture~DNLn)  
summary(lmDNLnTexture)  
anova(lmDNLnTexture)
```

```
lmDNLnOlsenP<-lm(OlsenP~DNLn)  
summary(lmDNLnOlsenP)  
anova(lmDNLnOlsenP)
```

```
lmDNLnTotalNLn<-lm(TotalNLn~DNLn)  
summary(lmDNLnTotalNLn)  
anova(lmDNLnTotalNLn)
```

```
lmDNLnAmmoniumLn<-lm(AmmoniumLn~DNLn)  
summary(lmDNLnAmmoniumLn)  
anova(lmDNLnAmmoniumLn)
```

```
lmDNLnNitrate<-lm(Nitrate~DNLn)  
summary(lmDNLnNitrate)  
anova(lmDNLnNitrate)
```

```
lmDNLnOrganicC<-lm(OrganicC~DNLn)  
summary(lmDNLnOrganicC)  
anova(lmDNLnOrganicC)
```

```
lmDOCLnTexture<-lm(Texture~DOCLn)
```

```
summary(lmDOCLnTexture)
```

```
anova(lmDOCLnTexture)
```

```
lmDOCLnOlsenP<-lm(OlsenP~DOCLn)
```

```
summary(lmDOCLnOlsenP)
```

```
anova(lmDOCLnOlsenP)
```

```
lmDOCLnTotalNLn<-lm(TotalNLn~DOCLn)
```

```
summary(lmDOCLnTotalNLn)
```

```
anova(lmDOCLnTotalNLn)
```

```
lmDOCLnAmmoniumLn<-lm(AmmoniumLn~DOCLn)
```

```
summary(lmDOCLnAmmoniumLn)
```

```
anova(lmDOCLnAmmoniumLn)
```

```
lmDOCLnNitrate<-lm(Nitrate~DOCLn)
```

```
summary(lmDOCLnNitrate)
```

```
anova(lmDOCLnNitrate)
```

```
lmDOCLnOrganicC<-lm(OrganicC~DOCLn)
```

```
summary(lmDOCLnOrganicC)
```

```
anova(lmDOCLnOrganicC)
```

```
lmTextureOlsenP<-lm(OlsenP~Texture)
```

```
summary(lmTextureOlsenP)
```

```
anova(lmTextureOlsenP)
```

```
lmTextureTotalNLn<-lm(TotalNLn~Texture)
```

```
summary(lmTextureTotalNLn)
```

```
anova(lmTextureTotalNLn)
```

```
lmTextureAmmoniumLn<-lm(AmmoniumLn~Texture)
summary(lmTextureAmmoniumLn)
anova(lmTextureAmmoniumLn)
```

```
lmTextureNitrate<-lm(Nitrate~Texture)
summary(lmTextureNitrate)
anova(lmTextureNitrate)
```

```
lmTextureOrganicC<-lm(OrganicC~Texture)
summary(lmTextureOrganicC)
anova(lmTextureOrganicC)
```

```
lmOlsenPTotalNLn<-lm(TotalNLn~OlsenP)
summary(lmOlsenPTotalNLn)
anova(lmOlsenPTotalNLn)
```

```
lmOlsenPAmmoniumLn<-lm(AmmoniumLn~OlsenP)
summary(lmOlsenPAmmoniumLn)
anova(lmOlsenPAmmoniumLn)
```

```
lmOlsenPNitrate<-lm(Nitrate~OlsenP)
summary(lmOlsenPNitrate)
anova(lmOlsenPNitrate)
```

```
lmOlsenPOrganicC<-lm(OrganicC~OlsenP)
summary(lmOlsenPOrganicC)
anova(lmOlsenPOrganicC)
```

```
lmTotalNLnAmmoniumLn<-lm(AmmoniumLn~TotalNLn)
summary(lmTotalNLnAmmoniumLn)
anova(lmTotalNLnAmmoniumLn)
```

```
lmTotalNLnNitrate<-lm(Nitrate~TotalNLn)
```

```
summary(lmTotalNLnNitrate)
```

```
anova(lmTotalNLnNitrate)
```

```
lmTotalNLnOrganicC<-lm(OrganicC~TotalNLn)
```

```
summary(lmTotalNLnOrganicC)
```

```
anova(lmTotalNLnOrganicC)
```

```
lmAmmoniumLnNitrate<-lm(Nitrate~AmmoniumLn)
```

```
summary(lmAmmoniumLnNitrate)
```

```
anova(lmAmmoniumLnNitrate)
```

```
lmAmmoniumLnOrganicC<-lm(OrganicC~AmmoniumLn)
```

```
summary(lmAmmoniumLnOrganicC)
```

```
anova(lmAmmoniumLnOrganicC)
```

```
lmNitrateOrganicC<-lm(OrganicC~Nitrate)
```

```
summary(lmNitrateOrganicC)
```

```
anova(lmNitrateOrganicC)
```

```
(Sediment~Olsen-P~(mg~P~kg^-1)))
```

```
lm_eqn = function(m) {
```

```
  l <- list(a = format(coef(m)[1], digits = 2),
```

```
    b = format(abs(coef(m)[2]), digits = 2),
```

```
    r2 = format(summary(m)$r.squared, digits = 3));
```

```
  if (coef(m)[2] >= 0) {
```

```
    eq <- substitute(italic(y) == a + b %.% italic(x)^*, "~~italic(r)^2~="~r2,l)
```

```
  } else {
```

```
eq <- substitute(italic(y) == a - b %.% italic(x)*,"~~italic(r)^2~="~r2,l)
}
```

```
as.character(as.expression(eq));
}
```

```
ggplot(PotholeData, aes(y=Texture, x=GPSEasting)) +
  xlab(expression(GPS~Easting~("UTM Zone 14N, NAD 1983")))) +
  ylab(expression(Sediment~texture~("% Clay")))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(250000,700000)) +
  scale_y_continuous(expand = c(0,0), limits = c(0,45)) +
  geom_text(x = 450000, y = 42, label = lm_eqn(lm(Texture ~
    GPSEasting)),parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))
```

```
ggplot(PotholeData, aes(y=AmmoniumLn, x=GPSEasting)) +
  xlab(expression(GPS~Easting~("UTM Zone 14N, NAD 1983")))) +
  ylab(expression(Ln~of~ammonium-N~(Ln~mg~NH[4]-N~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(250000,700000)) +
  scale_y_continuous(expand = c(0,0), limits = c(0,4.5)) +
  geom_text(x = 520000, y = 4.2, label = lm_eqn(lm(AmmoniumLn ~
    GPSEasting)),parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
```

```

panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=ConductivityLn, x=GPSNorthing)) +
  xlab(expression(GPS~Northing~("UTM Zone 14N, NAD 1983")))) +
  ylab(expression(Ln~of~conductivity~(Ln~mu*S~cm^-1)))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(5400000,5700000),
                     breaks = c(5400000, 5500000, 5600000, 5700000),
                     labels=c("5.4e+06","5.5e+06","5.6e+06","5.7e+06")) +
  scale_y_continuous(expand = c(0,0), limits = c(5,8.5)) +
  geom_text(x = 5600000, y = 8.3, label = lm_eqn(lm(ConductivityLn ~ GPSNorthing)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=DOCLn, x=GPSNorthing)) +
  xlab(expression(GPS~Northing~("UTM Zone 14N, NAD 1983")))) +
  ylab(expression(Ln~of~DOC~(Ln~mg~DOC~L^-1)))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(5400000,5700000),
                     breaks = c(5400000, 5500000, 5600000, 5700000),
                     labels=c("5.4e+06","5.5e+06","5.6e+06","5.7e+06")) +
  scale_y_continuous(expand = c(0,0), limits = c(3.5,5.8)) +
  geom_text(x = 5580000, y = 5.7, label = lm_eqn(lm(DOCLn ~ GPSNorthing)),
            parse=TRUE, colour="black", size = 4) +

```

```

theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=DOCLn, x=LengthLn)) +
xlab(expression(Ln~of~transect~length~(Ln~m))) +
ylab(expression(Ln~of~DOC~(Ln~mg~DOC~L^-1))) + geom_point() +
geom_smooth(method="lm", fullrange=TRUE) +
scale_x_continuous(expand = c(0,0), limits = c(0,4)) +
scale_y_continuous(expand = c(0,0), limits = c(3.5,5.8)) +
geom_text(x = 1.5, y = 5.7, label = lm_eqn(lm(DOCLn ~ LengthLn)),
parse=TRUE, colour="black", size = 4) +
theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=TotalNLn, x=LengthLn)) +
xlab(expression(Ln~of~transect~length~(Ln~m))) +
ylab(expression(Ln~of~total-N~(Ln~mg~N~kg^-1))) + geom_point() +
geom_smooth(method="lm", fullrange=TRUE) +
scale_x_continuous(expand = c(0,0), limits = c(0,4)) +
scale_y_continuous(expand = c(0,0), limits = c(7,10)) +
geom_text(x = 1.5, y = 9.85, label = lm_eqn(lm(TotalNLn ~ LengthLn)),
parse=TRUE, colour="black", size = 4) +
theme(axis.line = element_line(colour = "black"),

```

```

axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=Nitrate, x=LengthLn)) +
  xlab(expression(Ln~of~transect~length~(Ln~m))) +
  ylab(expression(Nitrate-N~(mg~NO[3]-N~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(0.6,4)) +
  scale_y_continuous(expand = c(0,0), limits = c(-0.95,5.5)) +
  geom_text(x = 1.8, y = 5.2, label = lm_eqn(lm(Nitrate ~ LengthLn)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=OrganicC, x=LengthLn)) +
  xlab(expression(Ln~of~transect~length~(Ln~m))) +
  ylab(expression(Organic-C~(mg~organic-C~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(0.6,4)) +
  scale_y_continuous(expand = c(0,0), limits = c(-10000,200000)) +
  geom_text(x = 2, y = 193000, label = lm_eqn(lm(OrganicC ~ LengthLn)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),

```

```

panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=DNLn, x=ConductivityLn)) +
  xlab(expression(Ln~of~conductivity~(Ln~mu*S~cm^-1))) +
  ylab(expression(Dissolved-N~(Ln~mg~DN~L^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(5,8.5)) +
  scale_y_continuous(expand = c(0,0), limits = c(0,3.2)) +
  geom_text(x = 6.4, y = 3, label = lm_eqn(lm(DNLn~ConductivityLn)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=DOCLn, x=ConductivityLn)) +
  xlab(expression(Ln~of~conductivity~(Ln~mu*S~cm^-1))) +
  ylab(expression(Ln~of~DOC~(Ln~mg~DOC~L^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(5,8.5)) +
  scale_y_continuous(expand = c(0,0), limits = c(3.5,5.8)) +
  geom_text(x = 6.3, y = 5.7, label = lm_eqn(lm(DOCLn~ConductivityLn)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),

```

```

panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=DOCLn, x=DNLn)) +
  xlab(expression(Ln~of~DOC~(Ln~mg~DOC~L^-1))) +
  ylab(expression(Dissolved-N~(Ln~mg~DN~L^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(0,4.8)) +
  scale_y_continuous(expand = c(0,0), limits = c(3.4,6.1)) +
  geom_text(x = 2, y = 5.8, label = lm_eqn(lm(DOCLn~DNLn)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=AmmoniumLn, x=Texture)) +
  xlab(expression(Sediment~texture~("% Clay"))) +
  ylab(expression(Ln~of~ammonium-N~(Ln~mg~NH[4]-N~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(0,45)) +
  scale_y_continuous(expand = c(0,0), limits = c(0,4.5)) +
  geom_text(x = 30, y = 4.3, label = lm_eqn(lm(AmmoniumLn~Texture)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),

```

```

panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=TotalNLn, x=OlsenP)) +
  xlab(expression(Sediment~Olsen-P~(mg~P~kg^-1))) +
  ylab(expression(Ln~of~total-N~(Ln~mg~N~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(0,40)) +
  scale_y_continuous(expand = c(0,0), limits = c(7,10)) +
  geom_text(x = 25, y = 9.8, label = lm_eqn(lm(TotalNLn~OlsenP)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=AmmoniumLn, x=TotalNLn)) +
  xlab(expression(Ln~of~total-N~(Ln~mg~N~kg^-1))) +
  ylab(expression(Ln~of~ammonium-N~(Ln~mg~NH[4]-N~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(7,10)) +
  scale_y_continuous(expand = c(0,0), limits = c(0,4.5)) +
  geom_text(x = 9, y = 4.3, label = lm_eqn(lm(AmmoniumLn~TotalNLn)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),

```

```

panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=OrganicC, x=TotalNLn)) +
  xlab(expression(Ln~of~total-N~(Ln~mg~N~kg^-1))) +
  ylab(expression(Organic-C~(mg~organic-C~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(6.9,10)) +
  scale_y_continuous(expand = c(0,0), limits = c(-30000,220000)) +
  geom_text(x = 8.5, y = 210000, label = lm_eqn(lm(OrganicC~TotalNLn)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

ggplot(PotholeData, aes(y=OrganicC, x=AmmoniumLn)) +
  xlab(expression(Ln~of~ammonium-N~(Ln~mg~NH[4]-N~kg^-1))) +
  ylab(expression(Organic-C~(mg~organic-C~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(0,4.5)) +
  scale_y_continuous(expand = c(0,0), limits = c(-30000,220000)) +
  geom_text(x = 2, y = 210000, label = lm_eqn(lm(OrganicC~AmmoniumLn)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

```

```

ggplot(PotholeData, aes(y=OrganicC, x=Nitrate)) +
  xlab(expression(Nitrate-N~(mg~NO[3]-N~kg^-1))) +
  ylab(expression(Organic-C~(mg~organic-C~kg^-1))) + geom_point() +
  geom_smooth(method="lm", fullrange=TRUE) +
  scale_x_continuous(expand = c(0,0), limits = c(0,5.5)) +
  scale_y_continuous(expand = c(0,0), limits = c(0,220000)) +
  geom_text(x = 2.5, y = 210000, label = lm_eqn(lm(OrganicC~Nitrate)),
            parse=TRUE, colour="black", size = 4) +
  theme(axis.line = element_line(colour = "black"),
        axis.text=element_text(colour="black"),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        panel.border = element_blank(),
        panel.background = element_rect(colour="black", fill="NA"))

```

**R code for hybrid cattail distribution model in 2011 pothole and ditch
marshes in southwestern Manitoba and southeastern
Saskatchewan**

```

filePath="C:/Users/Jen/Documents/Cattail/Data/"
fileName=paste(filePath,"2011CattailAll.csv",sep="")
PotholeData=read.table(fileName, header=TRUE, sep=",") #import data file

library(car)
library(ggplot2)

summary(PotholeData) #summarize data, calculate means, quantiles

palette(gray(seq(.3,.9,len=25))) #change palette to grayscale

```

Txglaucha=(PotholeData\$Txglaucha)
Tlatifolia=(PotholeData\$Tlatifolia)
TxglauchaP=(PotholeData\$TxglauchaP)
Texture=(PotholeData\$Texture)
OrganicC=(PotholeData\$OrganicC)
OrganicCLn=(PotholeData\$OrganicCLn)
TotalN=(PotholeData\$TotalN)
TotalNLn=(PotholeData\$TotalNLn)
Ammonium=(PotholeData\$Ammonium)
AmmoniumLn=(PotholeData\$AmmoniumLn)
Nitrate=(PotholeData\$Nitrate)
NitrateSQRT=(PotholeData\$NitrateSQRT)
OlsenP=(PotholeData\$OlsenP)
OlsenPSQRT=(PotholeData\$OlsenPSQRT)
Conductivity=(PotholeData\$Conductivity)
ConductivityLn=(PotholeData\$ConductivityLn)
pH=(PotholeData\$pH)
DN=(PotholeData\$DN)
DNLn=(PotholeData\$DNLn)
DOC=(PotholeData\$DOC)
DOCLn=(PotholeData\$DOCLn)
GPSNorthing=(PotholeData\$GPSNorthing)
GPSEasting=(PotholeData\$GPSEasting)
Date=(PotholeData\$Date)
Length=(PotholeData\$Length)
LengthLn=(PotholeData\$LengthLn)
LandUse=(PotholeData\$LandUse)
LandUseC=(PotholeData\$LandUseC)
Type=(PotholeData\$Type)
Litter=(PotholeData\$Litter)

```

LitterSQRT=(PotholeData$LitterSQRT)

# Null Model
MNull <- glm(cbind(Txglauca,Tlatifolia) ~ 1,
family = quasibinomial (link=logit),
data = PotholeData)
summary(MNull)

MDate<-glm(cbind(Txglauca,Tlatifolia)~Date,
family = quasibinomial, data = PotholeData)
summary(MDate)
anova(MNull, MDate, test="F")

MGPSEasting<-glm(cbind(Txglauca,Tlatifolia)~GPSEasting,
family = quasibinomial, data = PotholeData)
summary(MGPSEasting)
anova(MNull, MGPSEasting, test="F")

MGPSNorthing<-glm(cbind(Txglauca,Tlatifolia)~GPSNorthing,
family = quasibinomial, data = PotholeData)
summary(MGPSNorthing)
anova(MNull, MGPSNorthing, test="F")

MConductivityLn<-glm(cbind(Txglauca,Tlatifolia)~ConductivityLn,
family = quasibinomial, data = PotholeData)
summary(MConductivityLn)
anova(MNull, MConductivityLn, test="F")

MpH<-glm(cbind(Txglauca,Tlatifolia)~pH,
family = quasibinomial, data = PotholeData)
summary(MpH)

```

```

anova(MNull, MpH, test="F")

MDNLn<-glm(cbind(Txglauca,Tlatifolia)~DNLn,
family = quasibinomial, data = PotholeData)
summary(MDNLn)
anova(MNull, MDNLn, test="F")

MDOCLn<-glm(cbind(Txglauca,Tlatifolia)~DOCLn,
family = quasibinomial, data = PotholeData)
summary(MDOCLn)
anova(MNull, MDOCLn, test="F")

MTexture<-glm(cbind(Txglauca,Tlatifolia)~Texture,
family = quasibinomial, data = PotholeData)
summary(MTexture)
anova(MNull, MTexture, test="F")

MOlsenP<-glm(cbind(Txglauca,Tlatifolia)~OlsenP,
family = quasibinomial, data = PotholeData)
summary(MOlsenP)
anova(MNull, MOlsenP, test="F")
#Percent explained deviance
100*(134.98-114.59)/134.98

PR1 <- predict(MOlsenP, type="response",
dispersion=2.736788, se = TRUE)

ggplot(PotholeData, aes(x=PotholeData$TxglaucaP, y=PR1$fit)) +
  xlab("Hybrid cattail distribution") +
  ylab("Fitted hybrid cattail distribution") + geom_point() +
  stat_smooth(method="glm", family="quasibinomial", se=TRUE) +

```

```

scale_x_continuous(expand = c(0,0), limits = c(-1,101), breaks=
c(0,17,33,50,67,83,100)) +
scale_y_continuous(expand = c(0,0), limits = c(0,1), breaks=c(0,0.25,0.5,0.75,1)) +
theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

MTotalNLn<-glm(cbind(Txglauca,Tlatifolia)~TotalNLn,
family = quasibinomial, data = PotholeData)
summary(MTotalNLn)
anova(MNull, MTotalNLn, test="F")

MAmmoniumLn<-glm(cbind(Txglauca,Tlatifolia)~AmmoniumLn,
family = quasibinomial, data = PotholeData)
summary(MAmmoniumLn)
anova(MNull, MAmmoniumLn, test="F")

MNitrateLn<-glm(cbind(Txglauca,Tlatifolia)~NitrateLn,
family = quasibinomial, data = PotholeData)
summary(MNitrateLn)
anova(MNull, MNitrateLn, test="F")

MOrganicC<-glm(cbind(Txglauca,Tlatifolia)~OrganicC,
family = quasibinomial, data = PotholeData)
summary(MOrganicC)
anova(MNull, MOrganicC, test="F")

MLitter<-glm(cbind(Txglauca,Tlatifolia)~Litter,

```

```

family = quasibinomial, data = PotholeData)
summary(MLitter)
anova(MNull, MLitter, test="F")

```

```

MLengthLn<-glm(cbind(Txglauca,Tlatifolia)~LengthLn,
family = quasibinomial, data = PotholeData)
summary(MLengthLn)
anova(MNull, MLengthLn, test="F")

```

```

MLandUse<-glm(cbind(Txglauca,Tlatifolia)~LandUseC,
family = quasibinomial, data = PotholeData)
summary(MLandUse)
anova(MNull, MLandUse, test="F")

```

```

P1<-glm(cbind(Txglauca,Tlatifolia)~Texture + AmmoniumLn + Nitrate +
OlsenP + DOCLn + pH + Date + Litter + LandUseC,
family = quasibinomial, data = PotholeData)
summary(P1)
vif(P1)
anova(MNull, P1, test="F")
anova(P1)

```

```

# DOCLn contributed the least to decreasing deviance, removed
P2<-glm(cbind(Txglauca,Tlatifolia)~Texture + AmmoniumLn + Nitrate +
OlsenP + pH + Date + Litter + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(P2)
vif(P2)
anova(MNull, P2, test="F")
anova(P2)

```

```
# AmmoniumLn contributed the least to decreasing deviance, removed
```

```
P3<-glm(cbind(Txglauca,Tlatifolia)~Texture + Nitrate +
OlsenP + pH + Date + Litter + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(P3)
vif(P3)
anova(MNull, P3, test="F")
anova(P3)
```

```
# Texture contributed the least to decreasing deviance, removed
```

```
P4<-glm(cbind(Txglauca,Tlatifolia)~Nitrate +
OlsenP + pH + Date + Litter + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(P4)
vif(P4)
anova(MNull, P4, test="F")
anova(P4)
```

```
# Date contributed the least to decreasing deviance, removed
```

```
P5<-glm(cbind(Txglauca,Tlatifolia)~Nitrate +
OlsenP + pH + Litter + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(P5)
vif(P5)
anova(MNull, P5, test="F")
anova(P5)
```

```
# LandUse contributed the least to decreasing deviance, removed
```

```

P6<-glm(cbind(Txglauca,Tlatifolia)~ Nitrate + OlsenP + pH + Litter,
family = quasibinomial(link="logit"), data = PotholeData)
summary(P6)
vif(P6)
anova(MNull, P6, test="F")
anova(P6)
#explained deviance
100*(134.976-96.561)/134.976
# Test for interactions
add1(P6, ~.^2,test="F")
#only one that is sig. is Nitrate:OlsenP try removing Nitrate and add in LandUse

P7<-glm(cbind(Txglauca,Tlatifolia)~ OlsenP + pH + Litter + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(P7)
vif(P7)
anova(MNull, P7, test="F")
anova(P7)
#explained deviance
100*(134.976-99.041)/134.976
add1(P7, ~.^2,test="F")

#P7 re-written as Full
Full<-glm(cbind(Txglauca,Tlatifolia)~ OlsenP + pH + Litter + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(Full)
anova(MNull, Full, test="F")
anova(Full)
vif(Full)
#Test variables by dropping one at a time

```

```
M1<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M1)  
anova(Full, M1, test="F")
```

```
M2<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M2)  
anova(Full, M2, test="F")
```

```
M3<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + LandUseC,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M3)  
anova(Full, M3, test="F")
```

```
M4<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + Litter,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M4)  
anova(Full, M4, test="F")
```

```
M5<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + Litter + LandUseC,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M5)  
anova(Full, M5, test="F")
```

```
M6<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + LandUseC,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M6)  
anova(Full, M6, test="F")
```

```
M7<-glm(cbind(Txglauca,Tlatifolia)~pH + Litter,
```

```

family = quasibinomial(link="logit"), data = PotholeData)
summary(M7)
anova(Full, M7, test="F")

```

```

M8<-glm(cbind(Txglauca,Tlatifolia)~pH + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M8)
anova(Full, M8, test="F")

```

```

M9<-glm(cbind(Txglauca,Tlatifolia)~Litter + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M9)
anova(Full, M9, test="F")

```

```

M10<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC + GPSEasting,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M10)
anova(Full, M10, test="F")

```

```

M11<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC +
GPSNorthing,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M11)
anova(Full, M11, test="F")

```

```

M12<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC +
ConductivityLn,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M12)
anova(Full, M12, test="F")

```

```

M13<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC + LengthLn,

```

```

family = quasibinomial(link="logit"), data = PotholeData)
summary(M13)
anova(Full, M13, test="F")

```

```

M14<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC + OrganicC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M14)
anova(Full, M14, test="F")

```

```

M15<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC + DNLn,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M15)
anova(Full, M15, test="F")

```

```

M16<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC +
AmmoniumLn,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M16)
anova(Full, M16, test="F")

```

```

M17<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC + Texture,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M17)
anova(Full, M17, test="F")

```

```

M18<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC + Nitrate,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M18)
anova(Full, M18, test="F")

```

```

M19<-glm(cbind(Txglauca,Tlatifolia)~OlsenP + pH + Litter + LandUseC + Date,

```

```

family = quasibinomial(link="logit"), data = PotholeData)
summary(M19)
anova(Full, M19, test="F")

#Exchange OlsenP with Nitrate because there is an interaction, test with Null
M20<-glm(cbind(Txglauca,Tlatifolia)~Nitrate + pH + Litter + LandUseC,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M20)
anova(MNull, M20, test="F")

#Full model with interactions
FI<-glm(cbind(Txglauca,Tlatifolia)~ Nitrate + OlsenP + pH + Litter + LandUseC +
Nitrate:OlsenP,
family = quasibinomial(link="logit"), data = PotholeData)
summary(FI)
anova(MNull, FI, test="F")
anova(FI)
vif(FI)
anova(FI, Full, test="F")

M21<-glm(cbind(Txglauca,Tlatifolia)~Nitrate + OlsenP + pH +Nitrate:OlsenP,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M21)
anova(FI, M21, test="F")

M22<-glm(cbind(Txglauca,Tlatifolia)~Nitrate + OlsenP + pH + Litter +
Nitrate:OlsenP,
family = quasibinomial(link="logit"), data = PotholeData)
summary(M22)
anova(FI, M22, test="F")

```

```
M23<-glm(cbind(Txglauca,Tlatifolia)~Nitrate + OlsenP + pH + LandUseC +  
Nitrate:OlsenP,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M23)  
anova(FI, M23, test="F")
```

```
M24<-glm(cbind(Txglauca,Tlatifolia)~Nitrate + OlsenP + Litter +  
Nitrate:OlsenP,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M24)  
anova(FI, M24, test="F")
```

```
M25<-glm(cbind(Txglauca,Tlatifolia)~Nitrate + OlsenP + Litter +  
LandUseC + Nitrate:OlsenP,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M25)  
anova(FI, M25, test="F")
```

```
M26<-glm(cbind(Txglauca,Tlatifolia)~Nitrate + OlsenP + LandUseC +  
Nitrate:OlsenP,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M26)  
anova(FI, M26, test="F")
```

```
M27<-glm(cbind(Txglauca,Tlatifolia)~Nitrate + OlsenP +  
Nitrate:OlsenP,  
family = quasibinomial(link="logit"), data = PotholeData)  
summary(M27)  
anova(FI, M27, test="F")
```

#Check influence of points

```

dfbetaPlots(Full,layout=c(2,3),main=NULL, grid=FALSE)

#residual plots
par(mfrow=c(2,2), mar=c(3, 2, 2, 2)) # get all plots on one page
plot(Full)

#Plot partial effects of terms in model
par(mfrow=c(2,2), mar=c(4, 4, 2, 2))
termplot(Full, se=TRUE, col.se="black", partial.resid=TRUE, col.term="blue",
col.res="black")

#Check influence of points
dfbetaPlots(FI,layout=c(3,3),main=NULL, grid=FALSE)

#residual plots
par(mfrow=c(2,2), mar=c(4, 4.5, 2, 2)) # get all plots on one page
plot(FI)

#Plot partial effects of terms in model
par(mar=c(4, 4, 2, 2))
termplot(FI, se=TRUE, col.se="black", partial.resid=TRUE, col.term="blue",
col.res="black")

PR2 <- predict(Full, newdata=NULL, type="response",
dispersion=2.809424, se = TRUE)

ggplot(PotholeData, aes(x=PotholeData$TxglaucaP, y=PR2$fit)) +
  xlab("Hybrid cattail distribution") +
  ylab("Fitted hybrid cattail distribution") + geom_point() +
  stat_smooth(method="glm", family="quasibinomial", se=TRUE) +

```

```

scale_x_continuous(expand = c(0,0), limits = c(-1,101), breaks=
c(0,17,33,50,67,83,100)) +
scale_y_continuous(expand = c(0,0), limits = c(0,1), breaks=c(0,0.25,0.5,0.75,1)) +
theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

PR3 <- predict(FI, newdata=NULL, type="response",
dispersion=2.928109, se = TRUE)

ggplot(PotholeData, aes(x=PotholeData$TxglaucaP, y=PR3$fit)) +
xlab("Hybrid cattail distribution") +
ylab("Fitted hybrid cattail distribution") + geom_point() +
stat_smooth(method="glm", family="quasibinomial", se=TRUE) +
scale_x_continuous(expand = c(0,0), limits = c(-1,101), breaks=
c(0,17,33,50,67,83,100)) +
scale_y_continuous(expand = c(0,0), limits = c(0,1), breaks=c(0,0.25,0.5,0.75,1)) +
theme(axis.line = element_line(colour = "black"),
axis.text=element_text(colour="black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.border = element_blank(),
panel.background = element_rect(colour="black", fill="NA"))

```