HYDROLOGICAL & BIOGEOCHEMICAL CONTROLS ON CALCAREOUS FEN ECOSYSTEMS

HYDROLOGICAL AND BIOGEOCHEMICAL CONTROLS ON CALCAREOUS FEN ECOSYSTEMS

By

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ABSTRACT

Calcareous fens are base cation-rich peatland ecosystems that support a diverse assemblage of vegetation. This study furthers our knowledge on these unique wetlands through the determination of the hydrological and biogeochemical processes governing calcareous fen ecosystem function. The growing season hydroperiod of three calcareous fens in close proximity to one another was found to be very different: some streamside locations were subject to water table fluctuations of just 10 cm, whereas other sites to > 1 m fluctuation. Only a small area of the three fens was subject to appreciable groundwater upwelling, contradicting previously held concepts. The Riparian Fen derived most of its water from the stream; with groundwater recharge and stream discharge the principal outlets. The Trough Fen was precipitation and evapotranspiration dominated, with moderate overbank flooding, and small groundwater discharge. The Basin Fen received half of its growing season water through groundwater discharge, with most water leaving through evapotranspiration. The subsurface flowpath direction and magnitude were variable among the calcareous fens and were subject to between-year flow reversals. Phosphorus was very limiting across most of the fen areas, and this was principally related to an association with calcium and magnesium in the fen pore-waters. Gradients of redox-sensitive solutes were detected at all sites, and were organized along the dominant hydrological flowpaths. Plant species richness and diversity within the calcareous fens were controlled by differential responses of individual species to *in situ* hydrological and biogeochemical gradients. Organic matter content in the surface peat and the duration of the initial saturation period to start the growing season proved to be the most useful metrics for determining plant species ranges/tolerances within the calcareous fens.

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PREFACE

This thesis consists of a series of manuscripts that have been submitted to academic journals for publication. Naturally, there is some repetition between the chapters, particularly the study site and methods descriptions; however, all results are unique. The text and figures are reprinted as they appear in the journal submissions, with the exception that references to figures and chapters have been standardized to the format of the dissertation. The work presented represents collaborative research and the specific contributions of the candidate are presented below. At the time of submission all work is the copyright of the author.

Chapter 2

Title: Extreme variability in water table dynamics in temperate calcareous fens: Implications for biodiversity

Authorship: Duval, T.P., Waddington, J.M.

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Chapter 3

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Chapter 5
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CHAPTER 1: INTRODUCTION

1.1 Calcareous Fen Ecosystem Function

Calcareous fens are wetlands fed principally by water rich in calcium, magnesium, and bicarbonate (Komor, 1994; Almendinger and Leete, 1998b), have accumulated more than 40 cm of peat (National Wetlands Working Group, 1997; Mitsch and Gosselink, 2007), and have near-surface soil and surface water pH in the range of 6.0 to 7.8 (Eggers and Reed, 1987; Bedford and Godwin, 2003). Dominated by sedges and brown mosses, calcareous fens exhibit very high vascular and non-vascular vegetation species richness and diversity (Motzkin, 1994; Johnson and Steingraeber, 2003), and serve as regional refugia for a number of rare plant taxa (Nekola, 2004; Bowles et al., 2005). They are also home to several endangered and regionally rare animal species, particularly amphibian, reptile, and insect species (Bedford and Godwin, 2003). As such, calcareous fens are key conservation and restoration targets in North America (Cooper and MacDonald, 2000; Amon et al., 2002) and Europe (Jansen et al., 1996; Lamers et al., 2002; Middleton et al., 2006). Despite the very high biodiversity value and regional importance of these wetland ecosystems, comparatively little research has been conducted on the underlying hydrological and biogeochemical processes controlling calcareous fen ecosystem development.

In particular, the methodology of previous research has limited the degree of detection and quantification of the full range of factors contributing to the maintenance and functioning of calcareous fens. Calcareous fen ecosystem function has previously been viewed from the "different from others" approach, most commonly along the rich-poor fen gradient in Alberta (Vitt and Chee, 1990), Colorado (Johnson and Steingraeber, 2003), Iowa (Nekola, 2004), New York (Godwin et al., 2002), the Biebrza River valley in Poland (Wassen et al., 1990; Verhoeven et al., 1996), the Westbroek polders of The Netherlands (Verhoeven et al., 1996), the Zwarte Beek in Belgium (Olde Venterink et al., 2001) and the Western Carpathians separating Slovakia from the Czech Republic (Hájková et al., 2004; Rozbrojová and Hájek, 2008). Apparently the only published work on calcareous fens in Ontario is the characterization of peatlands in northern Ontario by Sjörs (1963). In order to assemble a large sample size for comparison between wetlands, each of these studies have sampled numerous fens and bogs but in very few locations and over very limited timescales (most commonly one site visit). Motzkin (1994) presents perhaps the most comprehensive survey of calcareous fens across a region (New England), but only documents the vegetation communities without reference to the underlying hydrological and biochemical conditions in those sites. These approaches are useful in delineating calcareous fens from other peatland types, but have failed to provide a comprehensive conceptual model of calcareous fen function.

There are however, a few examples of detailed investigations of single calcareous fens that have informed our understanding of these unique ecosystems. Boyer and Wheeler (1989) discovered vegetation was low in stature but more diverse near points of groundwater discharge in Bradley Moore Fen in the UK, with species richness decreasing but plants growing taller with increasing distance from the seepage track. These findings were related to increased calcium carbonate precipitation and increased water pH in the discharge zones, leading to lower phosphate bioavailability. In a Massachusetts sloping calcareous fen Picking & Veneman (2004) found similar results that high species richness was related to decreased pore-water mineral and carbonate content and a lack of surface ponding. In an Illinois calcareous prairie fen Bowles et al. (2005) found vegetation community shifts were related to organic matter and base cation content, but the area of greatest calcium carbonate precipitation held the lowest species richness and diversity. Cooper (1990) documented similar patterns in a Colorado montane calcareous fen, though the low species richness area also had high salt precipitation. Despite the latter two studies, the notion that sites of calcite precipitation host the greatest species richness and diversity prevails.

In part, this preconception is due to the equally held tenet that calcareous fens are formed directly at points of alkaline groundwater discharge (Amon et al., 2002; Almendinger and Leete, 1998b). At these points in the calcareous fens, discharging groundwater rich in $CaCO_3$ equilibrates with the atmosphere, causing a reduction in pCO_2, which leads to calcite precipitation (Almendinger and Leete, 1998a; Miner and Ketterling, 2003). However, Komor (1994) found a marked increase in calcite precipitation at locations distant from the discharge point, beginning at 5 cm depth, which corresponded to the average depth of the water table in the studied Minnesota fen (presumably the water table falls, decreasing pCO_2 in the now unsaturated sediments, promoting calcite precipitation). Despite the evidence that calcium carbonate precipitation is not limited to zones of groundwater discharge and that these areas are not always the locations of high species diversity, the current conceptual model of calcareous fen functioning still holds this as dogma, as presented below.

1.2 Calcareous Fen Conceptual Model

Based on a review of the literature a conceptual model of calcareous fens emerges. In presentation, the top-down approach of Mitsch and Gosselink (2007) is followed: the climate and geology determine where in the landscape calcareous fens can form, and also dictates the hydrological regime; this site hydrology then controls the development of the physiochemical soil environment; together, the hydrology and biogeochemistry predetermine the range of species capable of thriving in the habitat; biotic feedbacks are then possible. Calcareous fens form in areas either of consolidated sedimentary bedrock (limestone or dolostone) or unconsolidated glacially deposited carbonate materials (Amon et al., 2002). Groundwater in this hydrogeologic setting is presumed to be regional, recharging in porous, elevated portions of the landscape (Komor, 1994), travelling through the geologic strata, whereupon topographic breaks and/or reductions in bedrock permeability generate persistent upward hydraulic gradients (Almendinger and Leete, 1998b). Groundwater discharge zones can form as seeps at breaks in slopes or on flat terrain (both can be lacustrine) (Amon et al., 2002). The sustained groundwater discharge then saturates the land, providing the opportunity for peat formation as either sloping fens or apron fens (Figure 1.1).

Hydrologically, the connection of this groundwater discharge zone to regional flowpaths is assumed to ensure a stable hydroperiod with the water table very near the ground surface for much of the year (Wassen et al., 1990; Kotowski et al., 2001), with minor summer water table drawdowns of no more than 30 cm (Johnson and Steingraeber, 2003), due to increased evapotranspirative demand (Almendinger and Leete, 1998a) (Figure 1.2). The hydroperiod is controlled by the various components of the site's water balance (Mitsch and Gosselink, 2007). Precipitation, evapotranspiration, surface and groundwater inflows and outflows, and soil storage properties (porosity, specific yield) all interact to produce a fen hydroperiod. The partitioning of water into the various components of a site's budget has profound implications for biogeochemical and ecological functioning (Woo and Rowsell, 1993; Mitsch and Gosselink, 2007). There are currently only three published studies of calcareous fen water balances: a 0.3 ha site in the Westbroek polder of The Netherlands (Koerselman, 1989); the 24 ha Bradley Moor Fen in the Chalk region of the UK (Gilvear et al., 1993); and the 1.5 ha MacLean Fen Preserve in New York State (Drexler et al., 1999). According to these studies, inputs of water to calcareous fens are dominated by groundwater, with outputs usually partitioned between surface outflow and evapotranspiration (Figure 1.3).

Biogeochemically, the implication of alkaline groundwater as the principal source water for calcareous fens is calcium carbonate precipitation as this supersaturated calcareous groundwater equilibrates with the atmosphere, producing distinct areas of surficial marl or tufa deposits (Gilvear et al., 1993; Almendinger and Leete, 1998a; Miner and Ketterling, 2003). As the source water radiates outward from these seepage points, it is progressively less and less supersaturated with respect to calcite, reducing the marl precipitation. Thus, a base rich gradient is set up with calcium concentrations and pH declining with increasing distance from the seepage point. Of particular note, it has been suggested that phosphate is also precipitated with calcium as apatite during calcite precipitation (Boyer and Wheeler, 1989). Recently, research on the biogeochemistry of fens in general has focussed not on the implications of the removal of phosphorus from bioavailable forms, but rather on the various strategies used to restore previously drained fens and how this impacts the phosphorus cycle (Geurts et al., 2009; Zak et al., 2009). Redox chemistry, particularly the role of the iron cycle in sequestering and releasing phosphate has been the focus of this attention (Lucassen et al., 2005, 2006; Boomer and Bedford, 2008).

Ecologically, the presumed constant base-rich groundwater input and relatively minor water table fluctuations allow for a distinct obligate wetland community to grow in calcareous fens (Motzkin, 1994; Picking and Veneman, 2004), and the scarcity of phosphorus prevents any one species from dominating the rest, resulting in a very rich and diverse community (Boyer and Wheeler, 1989; Bowles et al., 2005). Several researchers have found that within-site species heterogeneity of this community is most strongly correlated with minor water table variations due to microtopography (Wassen et al., 1990; Johnson and Steingraeber, 2003; Nekola, 2004; Schröder et al., 2005). It does not appear as though any research has been conducted on the biotic feedbacks to the hydrology or biogeochemistry of calcareous fens.

1.3 Problems with the Current Conceptual Model

While the current conceptual model is based on a relatively extensive body of literature, several oversimplifications, inconsistencies and knowledge gaps exist. The hydrogeologic setting framework for calcareous fen formation presupposes regions of groundwater discharge are necessary (Amon et al., 2002; Godwin et al., 2002); thus, an *a priori* exclusion criterion is implied in the detection, classification and study of these systems. The tenet of a stable water table is primarily based on studies of multiple sites in a region sampled in just a few locations over a very short period of time all in the same timeframe (Johnson and Steingraeber, 2003; Nekola, 2004) and/or in very small sites; that is, past methodology has constrained the likelihood of a new epistemology. A flat hydroperiod implies a water balance as described in Figure 1.3 with groundwater dominance; however, the sample size leading to this conclusion is very small, and there is evidence of other components of the water balance being significant, particularly the influence of adjoining streams (Koerselman, 1989; Komor, 1994; Godwin et al., 2002).

If the geological and hydrological functioning of calcareous fens differs or is more complex than previously suggested, than it is entirely possible (probable) that the biogeochemistry may differ as well. Clearly the disparate findings on the role of a marl flat (cf. Boyer and Wheeler, 1989; Johnson and Steingraeber, 2003) suggest not all calcareous fens process base cations and nutrients similarly. Most pressing seems to be the relative role of calcium carbonate- and iron-mediated removal of phosphate from the fen pore-water. Finally, the manner in which the hydrological and biogeochemical processes of calcareous fens affect species diversity requires a more refined approach. The grab-and-bag approach of characterizing a range of fens of varying minerotrophic status has definitely increased our understanding of between-fen species diversity and its environmental controls, but has only contradicted the presupposed stable water table notion through demonstrating within-site species variation is most related to water level variation (Hájková et al., 2004). Further complicating a process-based understanding of species dynamics, the intense studies of vegetation patterns in single calcareous fens have primarily focussed on the biogeochemical gradients (Cooper, 1990; Bowles et al., 2005). Improvement of the conceptual model of calcareous fens will aid not only our understanding of natural environmental systems functioning, but also our management strategies as they apply to calcareous fen conservation, restoration, and creation.

1.4 Study Objectives

The overall aim of this study was to improve and refine the conceptual model of calcareous fen functioning by undertaking an intense spatial and temporal investigation of the dominant hydrological and biogeochemical processes in calcareous fens and their resultant controls on plant species diversity in a regional groundwater recharge watershed, which is a hydrogeological setting that theory suggests should not support calcareous fens. A suite of hydrometric monitoring equipment was used in conjunction with peat and pore-water sampling and vegetation surveying to achieve this objective. Because the goal was to improve our understanding of the most important function of calcareous fens, namely their high biodiversity and regional refuge for species, the growing season was targeted for analysis. Hydrological measurements were made year round from May 2006 to December 2008, though only May-October of each year is presented here. Because of logistical constraints, biogeochemical characterization was only undertaken in the growing seasons of 2006 and 2008, and only the 2008 data are reported here. A full vegetation survey and accompanying hydrological and biogeochemical characterization was made at the peak of the 2006 growing season.

Within this framework, the specific objectives of this study were:

1) to determine the range of variability of the growing season water table within calcareous fens, and to characterize the hydrodynamics of the peat profile in three contrasting growing seasons (Chapter 2);
2) to determine the water balance and subsurface flowpaths and fluxes of three calcareous fens in three contrasting growing seasons (Chapter 3);
3) to determine the controls on the bioavailable nutrient dynamics in calcareous fens and how they vary throughout the fens and the growing season (Chapter 4); and,
4) to determine the hydrological and biogeochemical controls on plant species diversity within calcareous fens, with an aim to find a method of analysis in keeping with ecological theory (Chapter 5).

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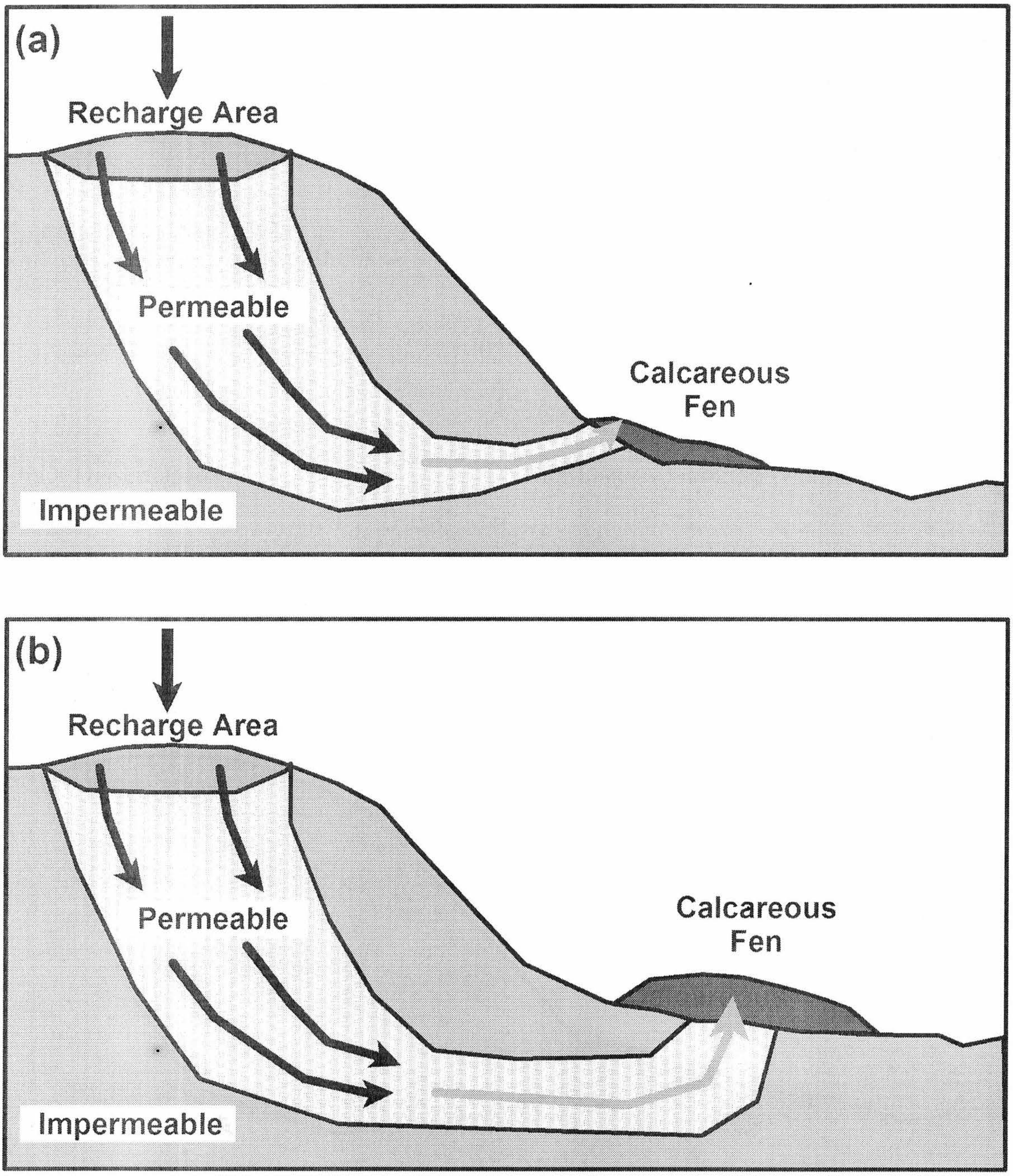

Figure 1.1: Idealized representation of hydrogeologic setting permitting calcareous fen formation, depicting (a) a slope fen and (b) a mound fen. Redrawn from Amon et al., 2002.

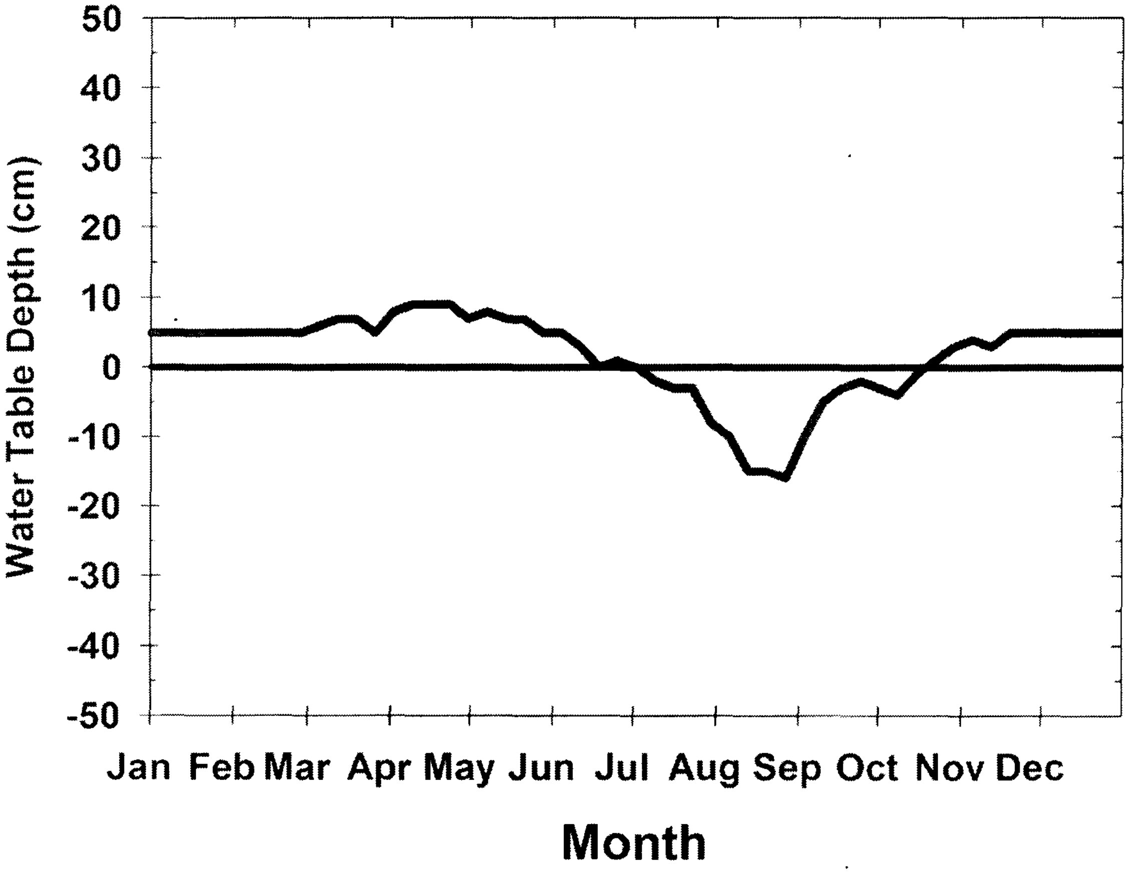

Figure 1.2: Hypothetical hydroperiod for a calcareous fen. Based on data provided in Koerselman, 1989 and Drexler et al., 1999a.

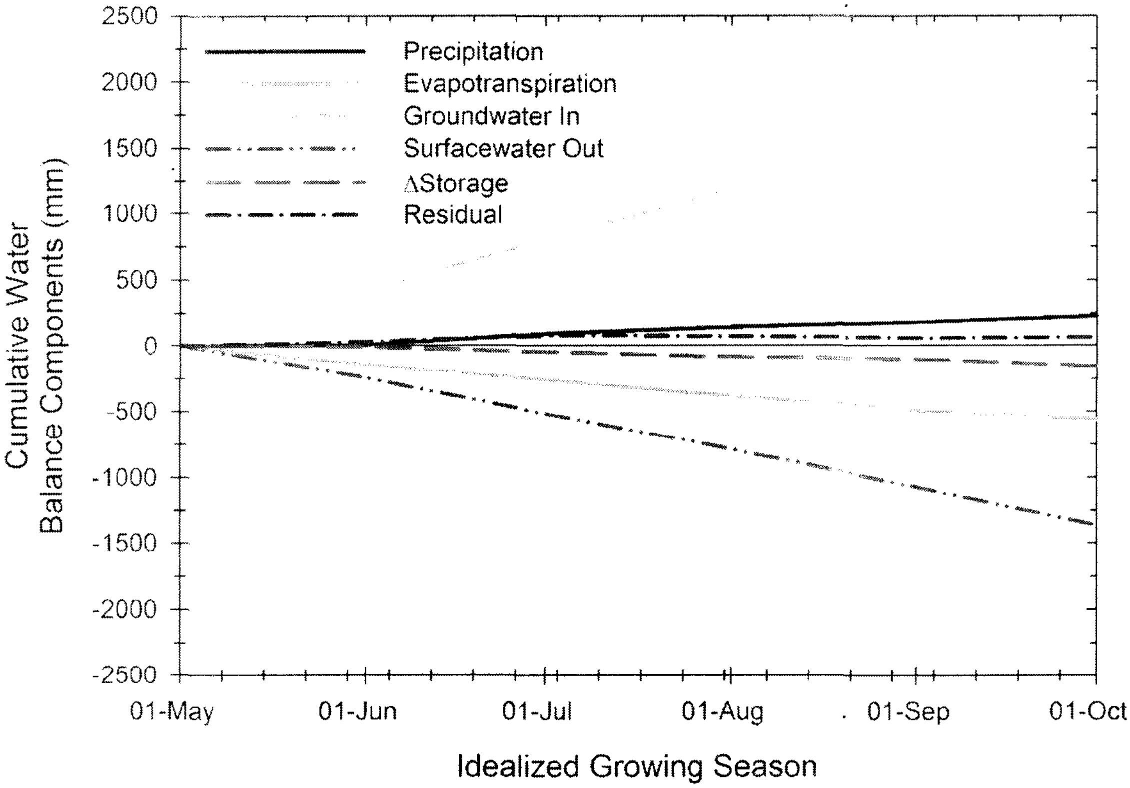

Figure 1.3: Hypothetical growing season water balance of a typical calcareous fen based on the current conceptual model, dominated by groundwater inputs and surface water outputs. Modified from data provided in Gilvear et al., 1993.

CHAPTER 2:
EXTREME VARIABILITY OF WATER TABLE DYNAMICS IN TEMPERATE CALCAREOUS FENS: IMPLICATIONS FOR BIODIVERSITY

2.1 Abstract

Calcareous fens are minerotrophic peatlands with very high species diversity, and maintenance of the water table is assumed to be a key contributor to this diversity. However, this assumption is based on limited study of fen water table dynamics. Here we monitor water table fluctuation and vertical hydraulic head gradients in distributed locations across three calcareous fens differing in hydrogeomorphic setting for three growing seasons. Water table position was extremely variable with absolute ranges of 89, > 100, and > 118 cm in the Riparian, Trough, and Basin Fens, respectively, and was controlled by landscape position and climate variability. Areas adjacent to a second order stream experienced the least water table fluctuation, while the Basin Fen, at > 75 m from a surface water connection, was very prone to year-to-year precipitation differences. Mean and median water table values were found to be poor indicators of biologically relevant hydroperiods. Piezometer nests varied in their hydrodynamics: the Riparian Fen displayed little variation in patterns between years, whereas the Trough Fen was subject to a significant alteration of peat hydrodynamics. Unlike most previous calcareous fen studies, upwelling groundwater was only prevalent in a small percentage of studied areas. Our results clearly demonstrate that there exist much more variation in calcareous fen hydrology than previously reported, and this variability has important implications for fen vegetation patterning and management.

2.2 Introduction

Calcareous fens are wetlands fed principally by water rich in calcium, magnesium, and bicarbonate (Komor, 1994; Almendinger and Leete, 1998b), have accumulated more than 40 cm of peat (National Wetlands Working Group, 1997; Mitsch and Gosselink, 2007), and have near-surface soil and surface water pH in the range of 6.0 to 7.8 (Eggers and Reed, 1987; Bedford and Godwin, 2003). Dominated by sedges and brown mosses, calcareous fens exhibit very high vascular and non-vascular vegetation species richness and diversity (Motzkin, 1994; Johnson and Steingraeber, 2003), and serve as regional refugia for a number of rare plant taxa (Nekola, 1994; Bowles et al., 2005). Despite the very high biodiversity value of these wetland ecosystems, little research has been conducted on the underlying hydrological processes controlling calcareous fen ecosystem development. In particular, the present study investigates the spatial and temporal variability in the position of the water table within calcareous fens.

Nutrient dynamics, especially P-limitation, have been correlated with the high species diversity of calcareous fens (Boyer and Wheeler, 1989; Vitt and Chee, 1990; Wells, 1996; van der Hoek et al., 2004; Rozbrojová and Hájek, 2008). While the role that hydrology has in controlling these nutrient dynamics in calcareous fens, through transport and redox-related transformations, has only recently been recognized (Lucassen et al., 2005, 2006; Bailey Boomer and Bedford, 2008), the maintenance and stability of the water table at the ground surface level in calcareous fens is considered a prime requirement for the diverse community of vegetation dominated by sedges and brown mosses (Wassen et al., 1990; Kotowski et al., 2001; Johnson and Steingraeber, 2003). This assumption is based on studies of calcareous fens that have only documented water table levels either at multiple sites a few times, or a few sites frequently (i.e., repeated measurement at one point in a fen). Recently, Hájkova et al. (2004) have suggested these disparate sampling regimes have led to an underestimation in the variability in environmental gradients such as water level; thus, measured relationships between water level and vegetation communities may not represent reality.

The seasonal fluctuation of a wetland's water table, the hydroperiod, is controlled by the various components of the site's water balance (Mitsch and Gosselink, 2007). Precipitation, evapotranspiration, surface and groundwater inflows and outflows, and soil storage properties (porosity, specific yield) all interact to produce a fen hydroperiod. While there is little research on the water balances of calcareous fens, inputs have been found to be dominated by groundwater, with outputs usually partitioned between surface outflow and evapotranspiration (Koerselman, 1989; Gilvear et al., 1993; Drexler et al., 1999b). Groundwater sources are assumed to be regional (Komor, 1994; Almendinger and Leete, 1998a; Amon et al., 2002); therefore, source inputs should remain constant from year to year, as should water table position. However, there is evidence that water table position does vary significantly between years (Johnson and Steingraeber, 2003) and between calcareous fens (Olde Venterink et al., 2001), suggesting variability in other portions of the water balance may represent important components of calcareous fen hydrology.

In this study we investigate the spatial and temporal variability in water table dynamics (hydroperiod and vertical hydraulic gradients) in three calcareous fens of southern Ontario, Canada, over three growing seasons. Specifically we seek to answer the following questions: (1) does the water table vary substantially within and between calcareous fens within close proximity to one another; (2) does the hydroperiod at a location vary from year to year; (3) are there variations in the hydraulic head distribution within the peat profile in space and time; and (4) what are the controls on any variability in these hydrodynamics?

2.3 Study Site

The three calcareous fens are located in a 332 ha headwater catchment of the Spencer Creek Watershed, 70 km west of Toronto, Ontario, Canada (Figure 2.1). The catchment spans 50 m of elevation, from 337 to 287 m above sea level and is underlain by fractured dolomite of the Guelph Formation (Upper Silurian in age). The northern half of the catchment contains 0 – 25 m of glacial till derived from the Galt Moraine northwest of the catchment. The till grades into outwash fine sands and silts at the northern boundary of the fens. The southern half of the catchment contains no glacial overburden and soils range from 0 – 60 cm thick. Upland vegetation consists primarily of *Thuja occidentalis* L. and *Betula papyrifera* Marsh. thickets interspersed by grass and shrubland. A series of groundwater seeps emerge mid-way down the catchment, which coalesce in a cedar swamp to form a clear, cold-water stream. This stream, Fletcher Creek, then flows through one of the calcareous fens, followed by a cedar swamp, then a cattail marsh at the outlet of the catchment. Historically, much of the glacial drift was excavated for gravel aggregate, resulting in steep hills in sections. Present land-use is a mixture of pasture and very low density residential.

For ease of comparison the unnamed fens are designated by their hydrogeomorphic position, using the nomenclature of Brinson (1993) and Godwin et al. (2002). At 4.5 ha the largest calcareous fen in the catchment is the Riparian Fen. It is bounded to the southwest by cedar swamp, the southeast and east by forested upland, the north by a railway, and the west by a county road. The Riparian Fen is gently sloping, with only 30 cm elevation change across 450 m of stream length (stream gradient of 0.00067). Vegetation of this site is variable, with the western half a mixture of fen sedges (*Carex flava* L., *C. livida* (Wahlenb.) Willd., *Rhynchospora alba* (L.) Vahl) and shrubs (*Rhamnus alnifolia* L'Hér., *Cornus stolonifera* Michx., *Rubus pubescens* Raf.), with isolated areas of *Thuja occidentalis* L. and *Larix laricina* (Du Roi) K. Koch trees. The eastern half is primarily sedge-dominated (*Carex aquatilis* Wahlenb., *C. prairea* Dewey ex Alph. Wood, *C. livida* (Wahlenb.) Willd.) with areas of *Menyanthes trifoliata* L., *Scirpus acutus* Muhl., and *Lysimachia thyrsiflora* L. co-dominance. A small pool occupies the southern-most portion, which is surrounded by calcite precipitate known as a marl flat (Miner and Ketterling, 2005). A radiocarbon date in the basal peat around the B2 piezometer nest found sustained peat initiation at 2320 ± 40 yBP.

The intermediate-sized fen is a Trough Fen. This long, thin 2 ha fen is bordered on the east by an upland thicket of cedar trees, to the north by the railway, which separates the fen from a marl-accumulating pond to the north, and to the west and south by a riparian cedar swamp. The minimum distance from the edge of the Trough Fen to Fletcher Creek is 20 m at points at the northernmost, middle, and southernmost portions of the fen. Elsewhere, the fen is separated from the stream by 40-75 m of riparian swamp. Vegetation in the Trough Fen is generally sedge-dominated (*Carex lacustris* Willd., *C. stricta* Lam., *C. lasiocarpa* Ehrh.) with co-dominance of grasses (*Calamagrostis canadensis* (Michx.) P. Beauv.) to the north, herbaceous species (*Eupatorium maculatum* L., *Lycopus uniflorus* Michx.) in the middle-north, rushes (*Juncus canadensis* J. Gay ex Laharpe) in the middle-south, and cattails (*Typha angustifolia* L.) in the south. There is 43 cm of elevation change along the 200 m length of the wetland.

The smallest wetland studied was the Basin Fen. It is 0.45 ha in size, and occupies a gentle depression in the upland cedar forest. There is at least 100 m of cedar upland or cedar swamp between the Basin Fen and Fletcher Creek, with no surface connection. The vegetation of the Basin Fen is sedge-dominated (*Carex stricta* Lam., *Carex utriculata* Boott, *Dulichium arundinaceum* (L.) Britton) with co-dominance of willow shrubs (*Salix pedicellaris* Pursh, *S. petiolaris* Sm.). Elevation of the fen floor varied by only 15 cm; however, the formation of tussocks of peat up to 70 cm above this fen floor by *C. stricta* led to a highly variable surface topography.

2.4 Methodology

A series of piezometer nests and wells were installed throughout the three calcareous fens to monitor hydraulic head and water table position (locations shown in Figure 2.1). Piezometers were constructed of 2.5 cm ID PVC piping with the bottom 10 cm slotted with 0.5 cm diameter perforations. The slot zone was screened with 250-μm diameter NITEX mesh. Piezometers were installed by auguring a hole to the desired depth using a 1-inch diameter soil auger and hammering in the piezometers. Each nest of piezometers consisted of four to six piezometers at nominal depths of 20, 40, 60, 80, 120, and 150 cm (depth reflects bottom of the slot zone). At some nest locations bedrock was reached prior to 120 cm depth; in those locations only the upper four piezometers could be installed. Each nest included at least one piezometer below the depth of peat into the mineral substratum. Wells were installed similar to the piezometers, and had perforations slotted throughout the peat profile and into the mineral substrate.

Hydraulic heads and water table depths were recorded approximately weekly during three growing seasons (May-October 2006-2008) For all measurements a single operator was used, and while precision was just 0.5 cm, the accuracy based on repeated measurements was found to be finer that this value. The measurement operator was positioned either on a constructed boardwalk or wooden skid located 50-75 cm from the piezometer nest. Repeated attempts to alter/distort the water depth recordings were unsuccessful when standing on the boardwalk. When using the smaller skid design water levels were found to fluctuate only in the 20 cm depth piezometers. Extreme care through consistent sampling location and weight distribution was taken to minimize any human error in measuring hydraulic head in these piezometers.

Individual piezometer nests were classified as locations of recharge, groundwater upwelling, lateral flow or focussed flow by comparing the hydraulic head of different depths to the water table following the procedure of Drexler et al. (1999a). Areas in which there was ≥ 2 cm deviation of hydraulic head per 50 cm depth in the peat profile were ascribed a classification of recharge, upwelling, or focussed flow. Nests were classified as recharge when hydraulic head values in the surface peat were greater than the water table elevation. Locations of upwelling or groundwater discharge had elevated hydraulic heads in the basal peat and/or mineral substrate relative to the water table. Focussed flow locations were those with elevated hydraulic heads in the middle of the peat profile, with similar to water table or lower hydraulic heads in the surface and basal areas of the nesting depth. This class was labelled "ill-defined" by Drexler et al. (1999a) as it could also be interpreted as having more than one dominant vertical gradient pattern. We introduce the term 'focussed' as the localized overpressure of hydraulic head creates an increase in the capacity for water flux relative to the upper or lower portions of the peat profile. Nests with < 2 cm deviation in hydraulic head per 50 cm depth were termed lateral flow, as in these areas the vertical component of water flux can be assumed to be negligible.

Temporal patterns of hydraulic head dynamics were depicted as seasonal trends with depth by interpolating between sampling dates. The Kriging method of interpolation was used in Surfer 7 (Golden Software, 1999). Spatial segregation of the hydraulic head classification scheme was conducted by assuming each piezometer nest was representative of an area between it and the nearest other nest(s). Vertical hydraulic gradients were calculated as the steady state maximum change in hydraulic head at each sampling date divided by the corresponding change in depth/elevation between those two points. Exceedance probabilities were calculated by dividing the rank of an individual water table measurement by the total number of measurements plus one in the respective classes, multiplied by 100 (see below for classes). For periods of less than weekly water table measurements, data were linearly interpolated to arrive at a continuous dataset.

2.5 Results

2.5.1 Climate Variability

Seasonally, 2006 (486.5 mm) and 2008 (544 mm) were wetter growing seasons than the 30-yr normal (432.4 mm) for a nearby climate station, whereas 2007 (213.6 mm) was an exceptionally dry growing season (Table 2.1). The 2008 growing season was the second wettest on record for the region (Environment Canada). Based on this, we characterize the 2006 growing season as 'Normal', the 2007 season as 'Dry', and the 2008 season as 'Wet'. There were monthly differences, however, as for example June 2006 was a very dry month, followed by a very wet July, in a normal growing season (Table 2.1). The mean daily temperature averages showed much less departure from the climate normals (Table 2.1). May 2008 was 2°C cooler than normal, whereas July 2006 and September 2007 were more than 1.5°C warmer than normal.

2.5.2 Water Table Fluctuation

The mean water table position suggested little difference between the fens: -4, -6.3, and –7 cm for the Riparian, Trough, and Basin Fens, respectively (Table 2.2). However, there was an 11.5 cm difference between the medians of the Riparian and Basin Fens for all years. Looking at individual years, the means and medians were almost identical in the wet 2008 growing season (Table 2.2), and both statistics concur with the full dataset that the Basin Fen was the wettest. The mean water tables for 2006 were lower than the medians by 3-5 cm, whereas in the dry year the mean was 3.4 and 20.5 cm higher than the median in the Riparian and Basin Fen, respectively, but 17 cm lower in the Trough Fen. Thus, for extremely wet years, when the water table can be expected to be above the ground surface for much of the growing season, the arithmetic mean of the water table data can approximate the 50th percentile (median) of where the water table resides in the fens, but this relationship becomes increasingly divergent as the sites dry out.

The absolute range in water table position increased with decreasing connectedness of the fens to the stream, from 89 cm in the Riparian Fen to > 118 cm in the Basin Fen (Table 2.2). There was a general trend of decreasing range in growing season water table position with increasing precipitation. The site-wide ranges, however, fail to provide an accurate depiction of the sites' water dynamics, as while the median of the Riparian Fen was similar to the median of piezometer nest D2 (0 cm 2006 and all years), the range of 66.5 cm in 2006 and 89 cm for all years was much greater than the 10 and 16 cm that occurred at D2 in 2006 and all years, respectively. That is, there was tremendous variability in the water table dynamics within the sites that cannot be captured by simple comparisons of basic statistics, and an evaluation of the hydroperiods at different locations is warranted.

The interannual variability in precipitation resulted in very different hydroperiods for the study sites, both between, and within the three calcareous fens. The normal, 2006 growing season indicated that water table fluctuation was variable depending on connection and distance to surface water bodies. Sites within the Riparian Fen adjacent to Fletcher Creek maintained a water table within ±5 cm of the ground surface for the entire growing season (A3 and D2 in Figure 2.2). On the other hand, areas within the Riparian Fen that were > 50 m from the stream, such as C1, had water tables > 30 cm below the ground for several weeks of the normal year growing season.

The Trough Fen also had variable hydroperiod dynamics among locations. The water table at F1 fell 20 cm during the very dry month of June 2006. A 56 mm rain event on 11 July 2006 resulted in a 13 cm rise in the water table. The water table at the F3 nest fell 30 cm through the month of June, rose to the ground surface in response to the July precipitation, and then rapidly fell to 60 cm below ground through the month of August. The Basin Fen had a hydroperiod similar to the F3 nest in the early part of the growing season of the normal year, falling 37 cm during the dry June and increasing 40 cm in response to the large July rain event. Unlike the F3 nest, however, water levels at the T1 nest did not fall back below the ground surface during 2006, remaining ~ 10 cm above the ground surface.

In the dry growing season of 2007 the influence of the stream on water table dynamics became especially apparent. As typified by nests A3 and D2, water levels close to the stream remained within 5 cm of the peat surface for the duration of the 2007 growing season (Figure 2.2). The water level in the marl flat of the Riparian Fen (nest D4) remained within 10 cm of the ground surface for the entire growing season. Nests C3 and F1 were subject to water table drawdowns of 60 cm through the growing season, near the depth of the peat layer in those areas. By the beginning of August 2007 the water table in the middle of the Trough Fen and within the Basin Fen (nests F3 and T1 in Figure 2.2, respectively) were greater than 80 cm below the ground surface, below our deepest installed piezometers. These water table depths were well below the peat depths of 40 cm in these areas, as well. The water table in the Basin Fen did not rise into the 80-cm deep piezometers until mid-November (data not shown).

Surface water was prevalent in the majority of the fen areas during the entire wet growing season of 2008. The Basin Fen was subject to 20 cm of standing water for the early growing season, and large mid-July 2008 precipitation events resulted in the water level nearly doubling to close to 40 cm above the ground (Figure 2.2). There was approximately 20 cm of standing water in the north end of the Trough Fen for the 2008 growing season while the middle of the Trough Fen experienced a water table at the ground surface for most of the growing season. Areas disconnected from the flowing stream of the Riparian Fen had a water table between 0 and 20 cm below ground during the first half of the growing season, with the increase in precipitation later in the year resulting in the water level remaining within ± 5 cm of the ground surface, whereas areas within 15 m of the stream maintained a water table ± 5 cm of the ground surface for the growing season. The marl flat of the Riparian Fen was unsaturated for only two weeks in this growing season, with the water level usually 10-15 cm above the ground surface.

The crossing properties of the hydroperiod with respect to the ground surface were calculated for the seven locations presented in Figure 2.2 (Table 2.3). The data indicated that there was marked variability in the duration of complete peat saturation between years, sites, and locations (nests). The Riparian Fen contained areas that were saturated for nearly all the growing season regardless of precipitation inputs (such as A3, Table 2.3), as well as areas that were rarely saturated in normal and dry years, and only 50 % of the wet year (C1, Table 2.3). Northern and southern portions of the Trough Fen, such as F1, were consistently saturated in normal and wet years (F1), but less than 50 % of the time in dry growing seasons. This was in contrast to the middle of the Trough Fen (F3), where even the wet year produced saturation for only 45 % of the growing season. The water level was above the basal ground surface in the Basin Fen for > 80 % of the 2006 season, all of the 2008 season, but only 30 % of the 22 week 2007 growing season (Table 2.3).

No nest location had the water level cross the ground surface more than 3 times during the growing season, with typically only 1 downcrossing below the peat surface (Table 2.3). Some areas of the study sites were subject to saturation for 2 to 3 months from the start of data collection in May of each year before the surface peat became unsaturated, whereas areas such as C1 and F3 only had between 1 and 4 weeks of saturation at the start of the growing season (Table 2.3). With the exception of the dry area surrounding nest C1, most periods with the water table below the surface lasted less than 1 month in the normal and wet years across the sites. However, during the dry 2007 growing season the duration of unsaturated conditions was predicated on the timing of the first, and only, downcrossing. Thus, during the dry conditions, the peat rooting depth was aerated for 2 to 5 months at all but the immediate streamside areas (Table 2.3).

2.5.3 Vertical Hydraulic Head Dynamics

In addition to the variable hydroperiods across the three calcareous fens, there were varied water dynamics through the peat profile. Recharge areas were characterized by hydraulic heads in the surface peat being greater than the water table, with decreasing hydraulic head with increasing depth. At nest E4, and similar nests, surface and near-surface water drains into the mineral substratum, such that at 1 m below the ground surface the hydraulic head is typically 6 to 8 cm below the water table in a normal year, and 9 to 10 cm in the dry year (Figure 2.3).

Only piezometer nests T1 and T2 in the Basin Fen demonstrated sustained patterns of groundwater upwelling (Figure 2.4). Hydraulic heads at 80 cm depth were generally 4 to 6 cm above the water table. This depth was 10 to 20 cm above the bedrock surface. These sites were also subject to increased hydraulic heads relative to water tables in the surface peat and lower head values at the peat-mineral contact around 35-40 cm. This latter phenomenon seems to be more pronounced during periods of maximum moisture deficit (e.g., mid-August of 2006) and/or low rainfall (e.g., late-May, 2008). The increased water tables of the wet year minimized the magnitude of this hydraulic head pattern, especially in August and September 2008, with both reduced hydraulic heads at depth relative to water table, and increased heads in the middle of the profile (Figure 2.4).

A few of the piezometer nests exhibited a lateral flow structure through the peat. In these nests, such as B3, which was 3 m from the stream, the hydraulic heads relative to the local water table were typically ±2 cm of the water table throughout the profile across three year's of data (Figure 2.5). This implies the overall horizontal hydraulic gradient through the fens imparted greater control of the flow dynamics at these locations. There was also a slight overpressure that developed at 40-80 cm depth in July and August 2006, and at 60-80 cm in May and August.

In contrast to the uniform hydraulic head profile of the lateral flow class, the focussed flow class was characterized by hydraulic heads similar to water table elevations in the upper peat profile, a zone of overpressure at 40-60 cm depth, and greatly decreased hydraulic heads in the mineral substrate (Figure 2.6). This groundwater class represented a large proportion of the study sites. The prevalent over-pressuring by 2 cm at 50-60 cm depth in the peat seemed to respond to precipitation events. This was especially true in the wet 2008 season where over-pressuring was present for the majority of the year. The zone of over-pressuring also partially collapsed in the very dry June 2006 (14 mm of rain).

The majority of the piezometer nests, though variable within and between years, maintained their overall classification; however, a few exhibited remarkable dependence on climate variability, such as piezometer nest F1 (Figure 2.7). Beginning in June of the normal 2006 an overpressure zone of 0.5-2 cm greater than the water table elevation developed beneath the peat-mineral contact. This hydraulic head relative to water table was greatest in June and July, but persisted through the year. The timing of the development of this zone was similar in the dry 2007, though of greater magnitude. After the disruption of the pattern in August 2007 when the water table fell below this zone, the over-pressuring was >3 cm above the water table at this depth. This higher magnitude was short-lived (one week) and the overpressure zone weakened as the year continued. In the wet 2008 however, this overpressure zone was dwarfed by the increased rain and water table elevation, as the pattern of hydraulic head relative to water table switched to resemble a recharge structure with higher hydraulic heads in the surface peat (Figure 2.7).

Figure 2.8 translates the distribution of the hydraulic heads in the peat profile to profile-wide vertical hydraulic gradients for each of the five classes of Figures 2.3-2.7. Piezometer nest B3 was classified as a location of lateral flow, and maintained a near constant but very small negative hydraulic gradient of -0.015 throughout the study period. Wet and dry periods had virtually no effect on the vertical hydraulic gradient of this area. Similarly, the recharge class, exemplified by the E4 nest maintained a near invariant vertical hydraulic gradient (VHG) throughout the three-year's of data collection. Typically the recharge class had a VHG of -0.06 (~4X greater than the lateral flow class). Both wet and dry periods resulted in a > 50 % increase in the magnitude of this gradient to -0.09-0.10, particularly in August of 2007 and 2008.

In these fens the upwelling piezometers, such as T1, responded to precipitation events (Figure 2.8). Under normal conditions the VHG tended to be +0.075, but extended periods with a lack of rainfall led to gradual declines in this value, such as June-July 2007, and rainfall causing increased VHG's. In 2006, the focussed flow areas, such as nest D1 also responded to rainfall events, but in a negative manner. A VHG of -0.033 was reduced through a wet May 2006 to -0.014, whereupon a lack of rain resulted in an increase (more negative) to -0.06. In the dry 2007, the VHG at D1 continually declined from -0.022 to -0.14. In 2008 the negative VHG at D1 remained fairly constant after the initial decrease in May.

The areas most influenced by climate fluctuations, such as nest F1, were the only areas where the VHG switched from positive to negative, both within and between growing seasons (Figure 2.8). At the start of June 2006 when data collection began, there was a negative VHG of -0.05 that quickly switched to positive values, reaching a maximum of +0.075 for the end of June-beginning of July. The data from 2007 suggested that this switching of direction of VHG in late May-early June is a common occurrence. The increased precipitation of 2008 in contrast, maintained a near constant -0.07 VHG at F1 for the entire growing season.

2.5.4 Spatial Arrangement of Hydrodynamics

By classifying all piezometer nests as recharge, upwelling, lateral, or focussed flow we found that the three fens behave more differently than suggested by water table statistics (Table 2.2). The majority of the Riparian Fen was comprised of focussed flow through the peat profile; that is, there was over-pressuring at some depth in the peat, with lower hydraulic heads in the underlying mineral substrate (Figure 2.9). The depth of the zone of over-pressuring varied from 40 to 80 cm, with no discernable pattern. Areas of surface water recharge beneath the peat into the underlying silt, fine sand, and/or bedrock occurred in 30 to 40 % of the Riparian Fen, with the increase in area stemming from decreased hydraulic heads at depth that resulted in a conversion from lateral flow in a few small areas during the dry year. There was a very small area of the Riparian Fen that was consistently a weak zone of groundwater upwelling.

The Trough Fen experienced marked changes in hydrodynamic class with changing climate conditions. In normal years the Trough Fen can be expected to be a split of focussed and lateral flow, with no major zones of upwelling or recharging (Figure 2.9). With the reduced water inputs and lower water table in the dry year, however, much of the lateral flow areas became either zones of recharge or upwelling. In the wet year (2008) the added water inputs dampened the localized area of focussed flow, which resulted in the conversion of that area to a zone of recharge. The Basin Fen was primarily an area of groundwater upwelling in the normal year (Figure 2.9). A water deficit in 2007 and water surplus in 2008 each caused a reduction in the area of upwelling; in 2007 this reduction was due to the lack of water throughout the catchment, whereas in 2008 the high water table minimized the contributions from below the peat.

With so little area of the calcareous fens influenced by groundwater discharge/upwelling, another control on the dynamic nature of the hydroperiods of the sites must exist. By categorizing the water table data from the nests not by their separate site locations but rather by proximity to the flowing stream, a key regulator of the water table position under varying growing season climatic conditions becomes apparent (Figure 2.10). We recognize that our invocation of exceedance probability on three years of data where two of those years are extreme deviations from the norm will distort the 'true' exceedance probabilities of water table position over a longer time period. Nevertheless, important generalities can be determined through such an analysis.

The immediate first 10 m adjacent to Fletcher Creek exhibited a very narrow distribution of water table position, regardless of year-to-year precipitation (Figure 2.10). In this near-stream zone the water table was at the ground surface for 50 % of the time studied. Also in this zone the water table never went above 10 cm nor did it drop below -20 cm. The shape of the curve is very similar for the area beyond 10 m and up to 25 m from the stream, with the 50th percentile still at the ground surface. However, at this increased distance from the stream channel, the wet year produced > 10 cm of standing water, and the dry year decreased the water table to < -20 cm, though for only short durations in each case (< 10 % of the time).

As the distance from the stream increases, the character of the water table increasingly deviated from the narrow range found closer to the stream. The water table still resided at the ground surface for 50 % of the time up to 50 m from the stream channel (Figure 2.10). At this distance, however, the water table was < -20cm for 20 % of the three growing seasons studied. The areas of the study sites that were separated from the stream by 50 to 75 m of linear distance were only saturated for 25 % of the time. Fully 35 % of the time the water table was < -20 cm, and was only > -40cm for < 80 % of the period of record. At distances greater than 75 m from the surface water body the water table dynamics did not resemble those closer to the stream. At this distance the calcareous fen areas were saturated for 70 % of the time. Furthermore, the water table exceeded 20 cm above ground 20 % of the time. On the other hand, once the water table dropped below ground level, it quickly fell deep into the peat and soil profile, not exceeding -20 cm for 23 % of the time, -40 cm 20 % of the time, and -80 cm 16 % of the time.

2.6 Discussion

2.6.1 Natural Variability in Water Availability

Our data demonstrate that there exists extreme natural variability in the growing season water table position of some calcareous fens, both within and between fens, even in close proximity to each other. The Riparian and Trough Fens were subject to 66.5 and 80 cm fluctuation in the position of the water table, respectively. Even the Basin Fen, at just 0.45 ha, experienced a 37 cm change throughout the growing season. These values are minima for the year, as they do not account for autumn precipitation and spring snowmelt, which would serve to increase the depth of standing water. Weather patterns can exacerbate or moderate this variability. Extreme water table drawdown of > 80 cm, especially in areas where peat depth was < 50 cm, occurred in the very dry 2007, whereas the very wet growing season reduced water table variability in the Riparian and Trough Fens by 30 and 60 %, respectively.

The absolute water table fluctuation documented in the present study is quite large compared to other calcareous fens studied. From three years of study Drexler et al. (1999a) found only a maximum 10-15 cm range in water tables, with most measurement locations subject to just a few centimetres fluctuation in a small kettle hole fen in New York. Based on a one-time measurement across 30 fens of New York, Godwin et al. (2002) found water table depths ranged from +1.9 to -19.2 cm. Water tables in Colorado calcareous fens were found to range by a maximum of 28 cm over three years (Johnson and Steingraeber, 2003). Maximum fluctuation over 2.5 years of study in a Dutch fen was 25 cm (Koerselman, 1989). Olde Venterink et al. (2001) however, did find between 50 and 60 cm variation in water levels over one year between a number of fens in the

Netherlands and Belgium. Other studies have demonstrated a dampening effect of surface level fluctuation in response to water level fluctuations in fens (Roulet, 1991; Price, 2003; Strack et al., 2006); however, peat deformation and ground surface elevation changes were undetectable in our fens (Waddington, unpublished data). It is probable the shallow peat depth and 'young' age of the peat in our study sites contributed to the large water table range.

In three successive growing seasons, variability in the controlling factor of precipitation and buffering of geomorphic position (connection to streamflow) resulted in distinct hydroperiods for the three studied fens. Our three year's of growing season water table data, in addition to sporadic winter water level measurements (data not shown), were not extensive enough to compute significant hydroperiod statistics (*sensu* Nuttle's (1997) harmonic mean approach). Nor were our data continuous enough to perform a proper analysis of crossing properties of the water table (*sensu* Bras & Rodriguez-Iturbe, 1994). However, we feel there is far more relevant water table information to wetland function than simply the mean or median, as is usually reported. As an example, comparison of Table 2.3 with Figure 2.2 reveals that several piezometer nests were subject to standing water for between 17 and 19 weeks of the growing season (A3 in 2007 & 2008, D2 in 2006 & 2008, and D4 in 2006), with seasonal mean values of 0.16, 1.84, 0.89, 1.32, and 6.2 cm, respectively; that is, only the D4 nest had a mean water table position more than 2 cm difference from the others in this example. However, the pattern of the hydroperiods were quite different, with a water level downcrossing of the ground surface occurring between 1 and 14 weeks from the start of the growing season in those nests in those years. We suggest this statistic, namely the time until the first downcrossing of the water level below the ground surface, is far more meaningful for understanding and predicting wetland processes than the mean water table position as it directly relates to the length of time until a major physiochemical shift of the peat soil caused by exposure to the atmosphere.

2.6.2 Peat Profile Hydrodynamics

Our data demonstrate the occurrence of focussed flow through the peat profile in a number of our piezometer nests, where zones of hydraulic head over-pressuring relative to the rest of the peat column developed, usually between 40-60 cm. Over-pressuring of porewater at depth in peatlands is a common phenomenon and can be persistent or develop seasonally (Devito et al., 1997; Rosenberry et al., 2003). Based on measures of specific conductivity, Drexler et al. (1999a) concluded connection to a regional groundwater system was responsible for the over-pressuring at their fen site. This line of evidence is not supported in our calcareous fens, as there were no marked deviations in specific conductivity in the areas of over-pressuring. Methodological problems, such as measurement error, sampling disturbance, blocked or leaking piezometers, were also unlikely, as respectively, measurements were made by the same operator and were consistent, measurements were made from a boardwalk and any disturbance would increase hydraulic head measurements in the 20-cm piezometer, and a few piezometers were replaced and/or duplicated to validate the measurements.

Entrapped gas formation, predominantly due to methane bubble formation, has been shown to increase hydraulic head in peat porewater at depth relative to the water table (Comas et al., 2005; Strack et al., 2006). It is also unlikely that this mechanism caused the detected over-pressuring in our piezometers, as piezometers have been shown to be unresponsive to this type of over-pressuring (Kellner et al., 2004), and indeed, recent research has suggested that piezometers installed in the peat can serve as conduits of methane to the atmosphere at this site (Waddington et al., 2009). Additionally, at our site, maximum rates of methane diffusion and ebullition occur in the marl flat area (Coulthard et al., 2009; Waddington et al., 2009), an area of persistent and dominant groundwater recharge. Variations in hydraulic conductivity can also lead to pressure variations in the peat profile, as from Darcy's Law, with constant discharge, an decrease in hydraulic conductivity will increase the hydraulic gradient, and vice versa. At nest D1, an area of focussed flow, hydraulic conductivity decreased an order of magnitude (10^{-3} to 10^{-4} cm s^{-1}) from the 20 cm piezometer to the 60 cm piezometer, then increased slightly at the 80 cm piezometer (Chapter 3). The lower hydraulic conductivity coincides with the zone of overpressure; therefore, we conclude that the zones of overpressure in our calcareous fens are due to decreases in hydraulic conductivity.

Unlike other studies, where patterns of hydraulic gradients varied seasonally at both the small piezometer nest scale (Drexler et al., 1999a) and/or the larger site scale (Devito et al., 1997; Johnson and Steingraeber, 2003), the calcareous fens in the present study demonstrated a more consistent pattern within a year. While the various piezometer nests displayed different patterns of vertical hydrodynamics across the sites, nearly all of the studied nests retained the same pattern seasonally, and the vast majority remained consistent between years (*e.g.*, the E4 nest remained a strong recharge nest throughout the study; Figures 2.3-2.6). These patterns were also reflected in the trend of vertical hydraulic gradients (Figure 2.8). We suggest the maintenance of these patterns, even in response to large precipitation variability and water table fluctuation, is in large part due to the overriding importance on hydrogeomorphology of the sites.

2.6.3 Water Source Areas of Calcareous Fens

It is generally assumed that calcareous fens receive the bulk of their water from groundwater sources (Boyer and Wheeler, 1989; Nekola, 1994; Picking and Veneman, 2008), usually connected to regional flow systems (Gilvear et al., 1993; Amon et al., 2002) and subject to very large positive vertical hydraulic gradients (Komor, 1994; Almendinger and Leete, 1998a). Only the Basin Fen displayed sustained groundwater upwelling in our study. That the Basin Fen was subject to a very large water table drawdown in the dry 2007 season, with the effective collapse of this upwelling, suggests the groundwater is locally, not regionally, derived. It is likely that this groundwater originates from local infiltration of precipitation into the surrounding cedar uplands, with subsequent emergence in the topographic low spot of the Basin Fen.

A 330 mm difference in growing season precipitation between dry and wet years resulted in large departures in water table levels in the study fens from a growing season with near-normal precipitation. The effect of this variability in climatic conditions was not consistent within the fens; in our study sites areas closer to Fletcher Creek were subject to smaller water table fluctuations than areas farther from the stream. Thus, the geomorphic influence of the stream overrode the influence of the climatic fluctuation in some areas. In other settings, it is likely that connection to more regional groundwater supply would provide a similar 'buffering' of water levels in abnormally dry years (Devito et al., 1996), though the effects of wetter-than-average conditions in that setting is uncertain. Regardless, our results confirm the importance of surface water bodies in regulating the water level and storage in calcareous fens during extremes in weather.

None of our three studied calcareous fens fall into the current conceptual model of formation and functioning. Our data provide evidence that calcareous fens can, and do, form in hydrogeologic settings other than regional groundwater discharge zones. Furthermore, the overriding influence of the stream position suggests that hydrogeomorphic setting is also a critical factor in the functioning of some calcareous fens. At greater than 75 m away, Fletcher Creek has no direct influence on the Basin Fen, and as such that fen is most susceptible to climate fluctuations and relies on precipitation to sustain local groundwater flow for its maintenance (Chapter 3). The Riparian Fen, on the other hand, receives the majority of its water from the stream through stream recharge and overbank flooding (Chapter 3). Fletcher Creek originates from a series of groundwater seeps ~ 100 m upstream of the Riparian Fen; therefore, while it is strictly surface water that feeds the fen, chemically it closely resembles the up-gradient groundwater source (Duval and Waddington, in prep). The Trough Fen also receives water from Fletcher Creek during high discharge events that flood the adjacent riparian swamp, but receives only minimal subsurface lateral contributions during lower discharge periods (Chapter 3).

2.6.4 Implications for Calcareous Fen Vegetation

Water table dynamics directly control a vast array of other physical and chemical conditions within wetlands, including, peat anoxia, peat accumulation, redox potential, and nutrient, mineral, and metal transformations and availability (Mitsch and Gosselink, 2007). These conditions, in turn, directly influence the ability of wetland vegetation to compete, grow, and reproduce (Keddy, 2000). Johnson and Steingraeber (2003) found water table dynamics to be the principal control on fen plant species composition in calcareous fens of Colorado. The dominant sedges of our sites, and indeed most calcareous fens, take advantage of early growing season saturation by completing most of their growth at this time, before other, taller species begin to grow and compete for resources such as light and nutrients (Bernard, 1980). Wetland sedge species are particularly adept at root aerenchyma formation and producing an oxidized root microlayer (Moog, 1998; Moog and Bruggeman, 1998). Herbaceous species, such as *Eupatorium maculatum* L., *Eupatorium perfoliatum* L., *Solidago uliginosa* Nutt., and *Aster borealis* (Torr. & A. Gray) Prov. do not mature until near the end of the growing season, after the period of water table drawdown. Kotowski et al. (2001) found that a sedge species, as well as other fen species tested, were more responsive to light levels than water depth. That is, sedges are adapted to sustain prolonged periods of saturation, but cannot tolerate crowding from other vegetation.

Additionally, the soil chemical environment is drastically affected by water table dynamics. The occurrence of nitrogen species and mineralization, nitrification, and denitrification rates are all tightly controlled by degree of saturation in calcareous wetlands (Van Hoewyck et al., 2000). Phosphorus dynamics, considered the principal limiting nutrient in calcareous fens leading to high species diversity, are also controlled by water level (Koerselman et al., 1993). Sulphate reduction to the toxic hydrogen sulphide gas under prolonged saturated conditions has been shown to affect fen species biomass (Geurts et al., 2009), as has Fe^{3+} reduction to Fe^{2+} leading to iron toxicity (Lucassen et al., 2000). All of these cycles have been shown to interact to affect peat chemistry and vegetation dynamics (Lucassen et al., 2005). Thus, detailed knowledge of water table dynamics, and how these dynamics may change due to disturbance or natural variability, can help explain and predict the distribution of the high diversity of calcareous fen communities.

Our determination of the water table exceedance probabilities relative to the stream can help with this explanation. In our calcareous fens the maximum rooting depth of the dominant sedge vegetation was 20 cm below ground surface (Duval, unpublished data). We also did not detect any grass or slender herbaceous plant roots below this layer. Shrubs such as the *Salix spp.* and *Cornus spp.*, as well as the more robust herbs had roots penetrate to 40 cm depth, with sparse tree roots extending farther in the peat. Figure 2.10 then demonstrates that the roots of the vegetation within 10 m of Fletcher Creek were never fully exposed to an unsaturated environment. At 10-25 m from the stream the roots became fully exposed to an aerobic environment for just <10 % of the study period (in the dry year). This exposure increased to 20 and 35 % of the growing seasons at 25-50 and 50-75 m from the stream, respectively. At 50-75 m from the stream plants with roots close to the surface only had to contend with saturated conditions for 25 % of the growing seasons studied. Plants in the Basin Fen, at > 75 m from the stream, were subject to wide-ranging conditions of saturation: the peat was inundated for 70 % of the growing seasons, but the roots were exposed to an aerated environment for between one-quarter and one-fifth of the growing seasons for sedges and shrubs, respectively (Figure 2.10).

2.6.4 Sensitivity to Climate Fluctuations

While the effects of year-to-year variability in precipitation on water table and hydraulic head dynamics in these calcareous fens have been described, the causes of the precipitation variability and the frequency of significant departures from the norm are important from a management perspective. Seasonal, yearly, and decadal cycles of precipitation in specific locations around the globe are in large part affected by a number atmospheric teleconnections linked to oceanic circulation. The effects of these teleconnections have been shown to presently affect wetland water levels in the southern hemisphere (Roshier et al., 2001; Zoffoli et al., 2008), as well as throughout the mid- to late-Holocene (Donders et al., 2005). While the effects of most of the teleconnections that influence southern Ontario precipitation patterns are most pronounced in the winter months, there is evidence that global climate teleconnections influenced the observed precipitation patterns.

The Pacific-North America (PNA) teleconnection was in a very strong positive state (2.21, 1.98, and 1.88, respectively) for July, August, and September 2007. Positive values of the PNA index are associated with a negative departure in precipitation for areas around the Great Lakes and upper US Midwest (CPC, 2010). The summer (JAS) 2007 mean PNA index of 2.02 was the highest growing season three-month average for the 60-year NOAA record. 2007 was also the only year on record with any three growing season months to have a PNA Index > +1.5. There were 20 growing season months (MJJAS) in the 60-year record to have PNA Indices > +1.5, and only 1958 and 1960 (both JJA) and 1993 (AMJ) had thee-month averages > +1.5 (all data obtained from NOAA). The seasonal (MJJAS) precipitation values for the Guelph station for 1958, 1960, and 1993 were 420.9, 355.3, and 406.8 mm, respectively: all were below the seasonal normal of 432.4 mm, though well above the 2007 low of 213.6 mm (NCDIA, 2010). Thus, there appears to be a link between calcareous fen water table position in southern Ontario and atmospheric teleconnections, but a strong, prolonged positive phase of the PNA is infrequent during late spring and summer, occurring only 4 times in the past 60 years.

Previous ENSO events have been shown to weakly affect growing season precipitation in the region of the study sites, with El Nino events reducing rainfall by up to -0.3 mm day^{-1} (MSC, 2010). A transition from a weak La Nina to a weak El Nino occurred through the 2006 northern hemisphere growing season (Bell and Halpert, 2007), which would not be expected to have a net effect on precipitation. The fall-winter 2006-07 seasons were a weak El Nino event (Bell and Halpert, 2008), and this may have also contributed to low rain in the following 2007-growing season. The 2008 wet growing season was preceded by a strong La Nina event (L'Heureux et al., 2009), which may have contributed to the increased precipitation. Bell (2008) determined that this La Nina event, combined with the influence of the Madden-Julian Oscillation, led to very high precipitation in the US Midwest, which contributed to severe flooding in June 2008.

Climate projections suggest an increase in winter and spring precipitation and a decrease in summer precipitation in southern Ontario (Christensen, 2007). This will likely be coupled with warming summer temperatures (Christensen, 2007). Therefore, it is likely that calcareous fens in the region will be subject to higher early-growing season standing water, with perhaps a lengthened period of time until the first downcrossing of the water table. This should enhance opportunities for many sedge species to grow, but also restrict lower-growing sedges and rushes due to the greater water depth. Additionally, with lower summer precipitation, the likelihood of an upcrossing of the water table relative to the ground surface during the growing season decreases, which will favour late-season growth of meadow shrubs and herbs. The overall impacts of a changing water table regime in calcareous fens (do sedges or shrubs outcompete) as a consequence of climate change is difficult to predict, but increased knowledge of the hydrogeomorphic controls on water table buffering will aid management decisions of these species rich ecosystems.

2.7 Acknowledgements

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Table 2.1: Climate data from Guelph Turfgrass Research Station, 20 km north of the study area for the study period and the 30-yr normal for the same location.

Precipitation (mm)	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Seasonal**
2006	93.5	14	183.5	52	143.5	486.5
2007	66.6	43	25.4	43.6	35	213.6
2008	62.5	81.5	203.5	84.5	112	544
Normal	79.9	76	88.5	95.9	92.1	432.4

Temperature (°C)	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Seasonal**
2006	12.8	17.6	21.6	18.6	13.7	16.9
2007	12.7	18.2	18.4	19.3	15.8	16.9
2008	10.1	17.9	19.6	17.4	14.9	16.0
Normal	12.3	16.9	19.7	18.6	14.2	16.3

Table 2.2: Water table summary statistics for the three calcareous fen study sites.

Site	**Year**	**Mean**[†]	**Median**	**Max**	**Min**	**Range**
Riparian	***2006***	-3.8	-1	14	-52.5	66.5
	2007	-10.6	-6	10.5	-67	77.5
	2008	2.6	3	22	-18	40
	All Years	-4	-0.5	22	-67	89
Trough	***2006***	-4.7	-1	20	-60	80
	2007	-21.1	-3.75	15	< -80	> 95
	2008	7.5	7.5	18	-17	35
	All Years	-6.3	3	20	< -80	> 100
Basin	***2006***	5.7	10	20	-17	37
	2007	-47	-67.5	22	< -80	> 102
	2008	22.7	21.5	38	6	44
	All Years	-7	11	38	< -80	> 118

[†] Values are cm relative to ground surface

Table 2.3: Hydroperiod water table – ground surface crossing properties for representative locations in the calcareous fens.

Nest	Year	Total Duration Saturated (weeks)*	Total Duration Unsaturated (weeks)	Timing of First Downcrossing (weeks)	Frequency of Downcrossings (/ season)	Average Downcrossing Duration (weeks)
Riparian Fen						
A3	*2006*†	21	1	11	1	1
	2007	17	5	7	2	4
	2008	19	3	4	2	1.5
C1	*2006*†	1	21	1	1	21
	2007	0	22	1	1	22
	2008	11	11	1	3	3.7
D2	*2006*	16	6	1	3	2.5
	2007	4	18	4	1	18
	2008	17	5	5	2	2.5
D4	*2006*	18	4	14	1	4
	2007	7	15	6	2	7.5
	2008	21	1	10	1	1
Trough Fen						
F1	*2006*†	20	2	8	1	2
	2007	8	14	8	1	14
	2008	22	0	~	0	0
F3	*2006*†	5	17	4	2	8
	2007	2	20	2	1	20
	2008	10	12	2	3	4
Basin Fen						
T1	*2006*†	18	4	6	1	4
	2007	7	15	7	1	15
	2008	22	0	~	0	0

*For the period 01-May to 30-Sep of each year.

†Data were linearly interpolated from mid-April water depth measurements (not shown) to 02-June-06 well measurement to estimate May-06 values.

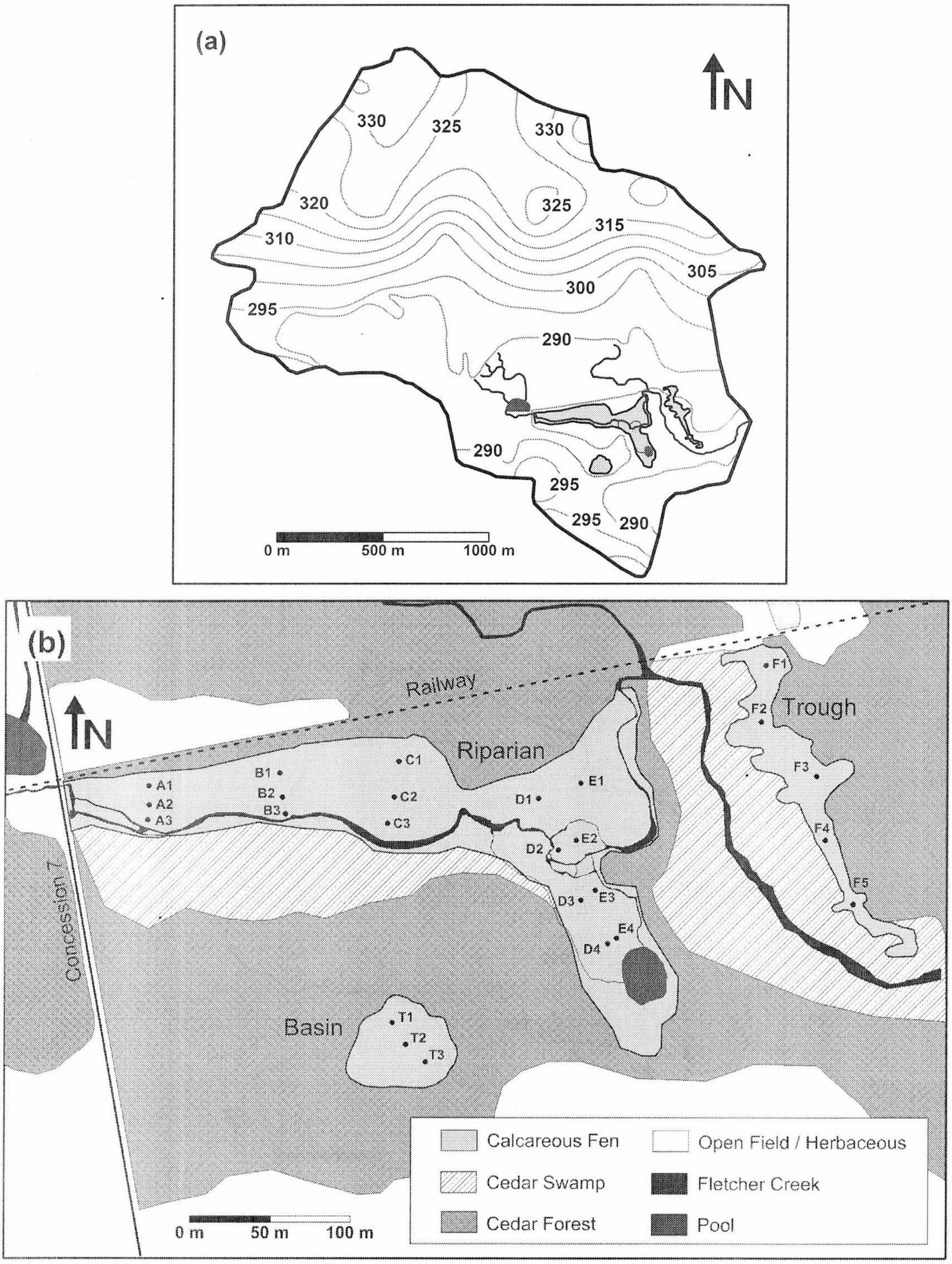

Figure 2.1: Study calcareous fens (a) within the Fletcher Creek Watershed and (b) detail of the Riparian, Trough, and Basin Fens and network of piezometer nests. Contour interval in (a) is 5 m.

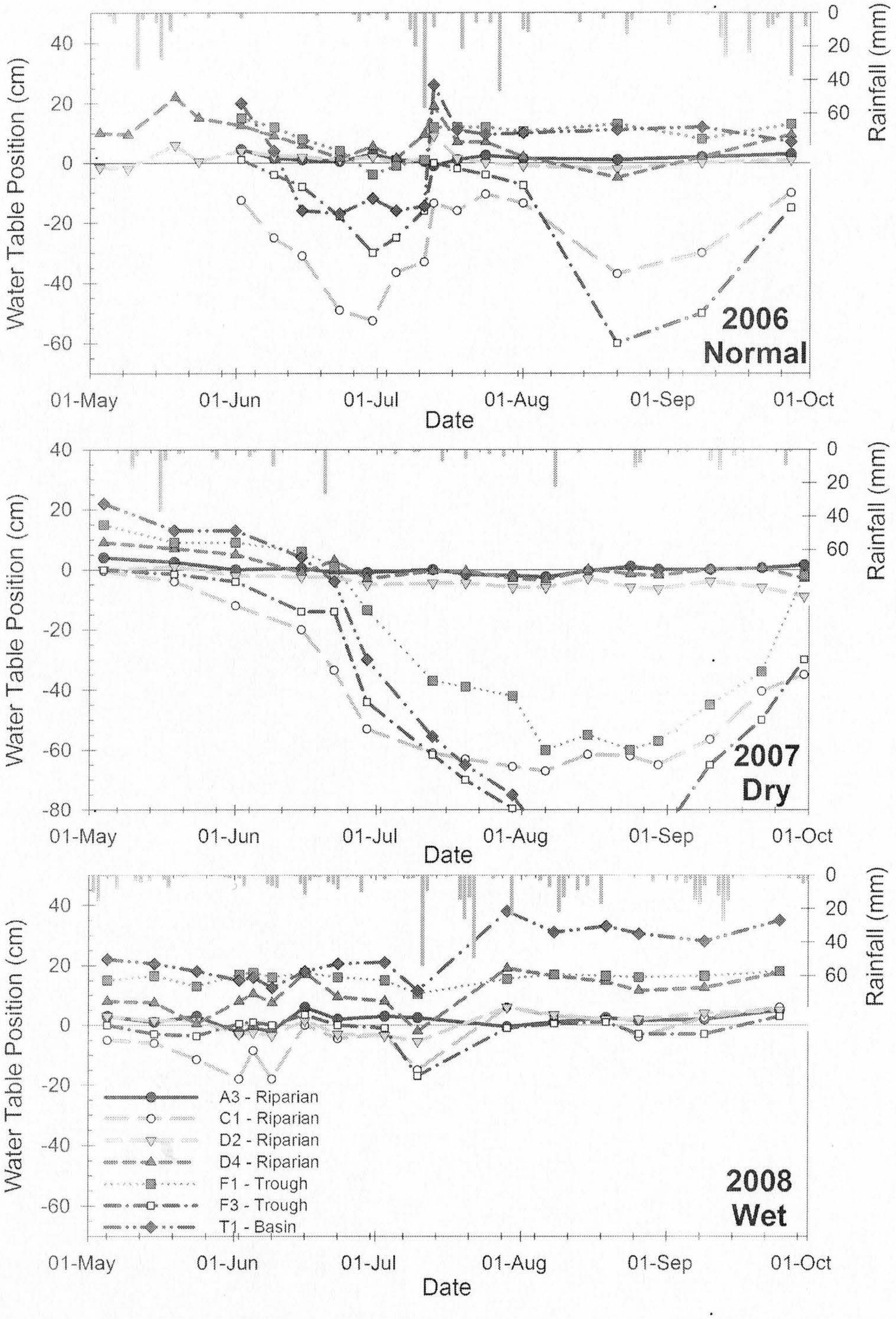

Figure 2.2: Water table fluctuation at selected locations in the three calcareous fens and precipitation in the 2006 ('Normal'), 2007 ('Dry'), and 2008 ('Wet') growing seasons.

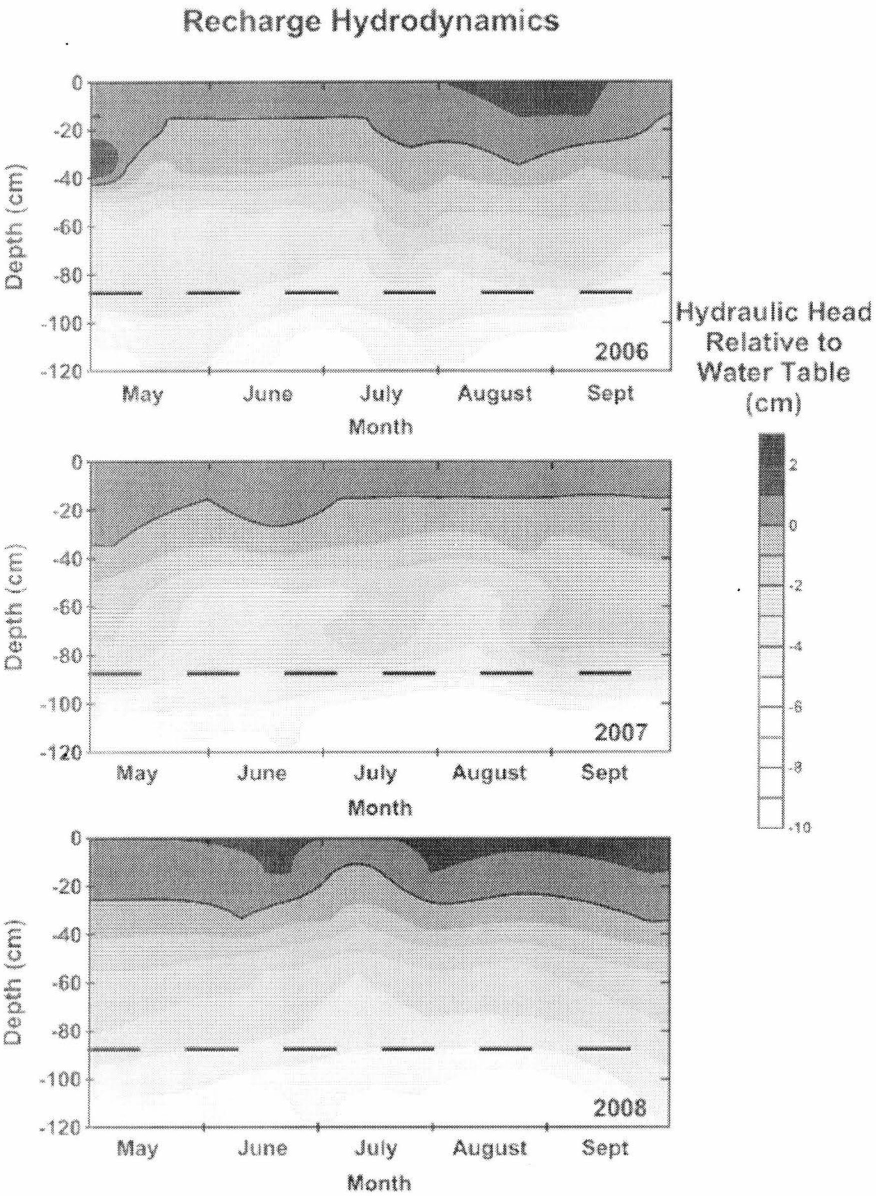

Figure 2.3: Representative seasonal hydraulic head relative to water table profiles through the peat and soil for the Recharge Class. The dashed line in each plot represents the depth of the peat layer at the nest depicted. The solid black line represents the equipotential with the water table, separating the transition from overpressure heads (dark) to underpressure heads (light).

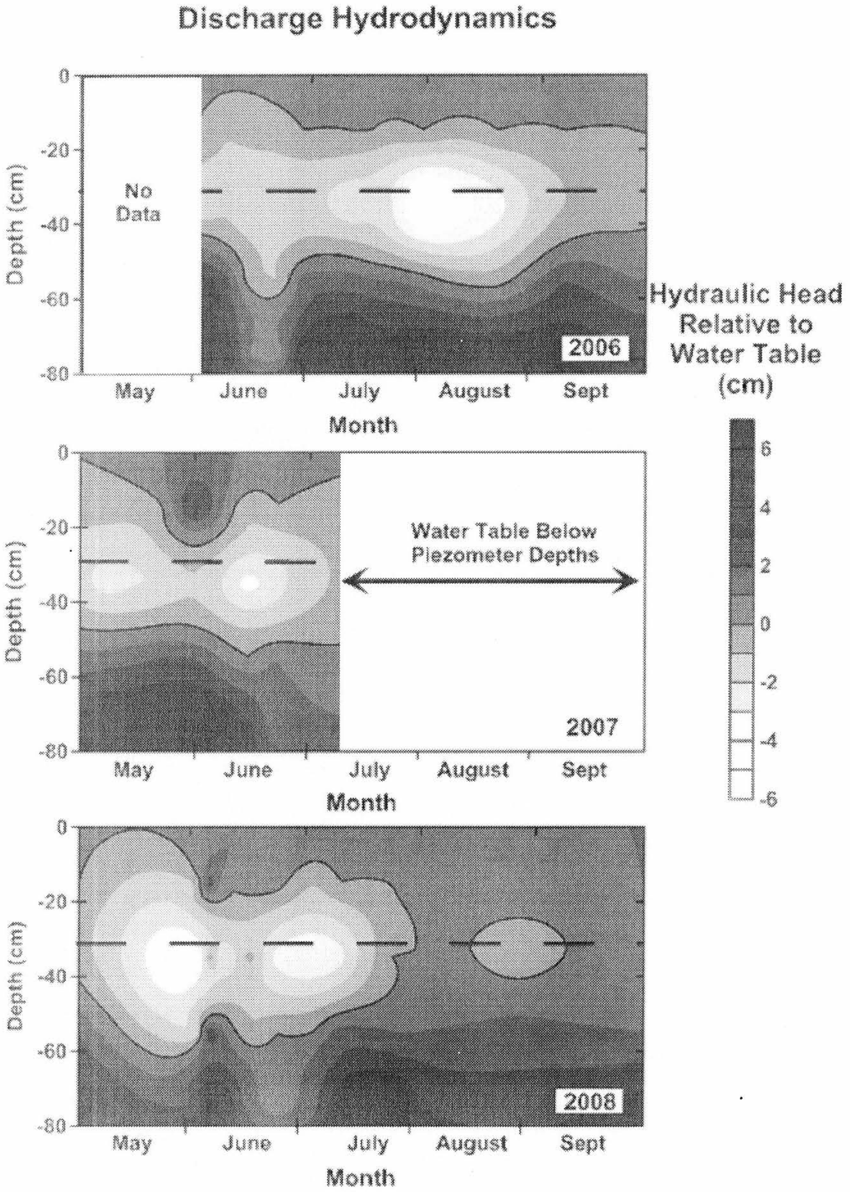

Figure 2.4: Representative seasonal hydraulic head relative to water table profiles through the peat and soil for the Discharge Class. The dashed line in each plot represents the depth of the peat layer at the nest depicted. The solid black line represents the equipotential with the water table, separating the transition from overpressure heads (dark) to underpressure heads (light).

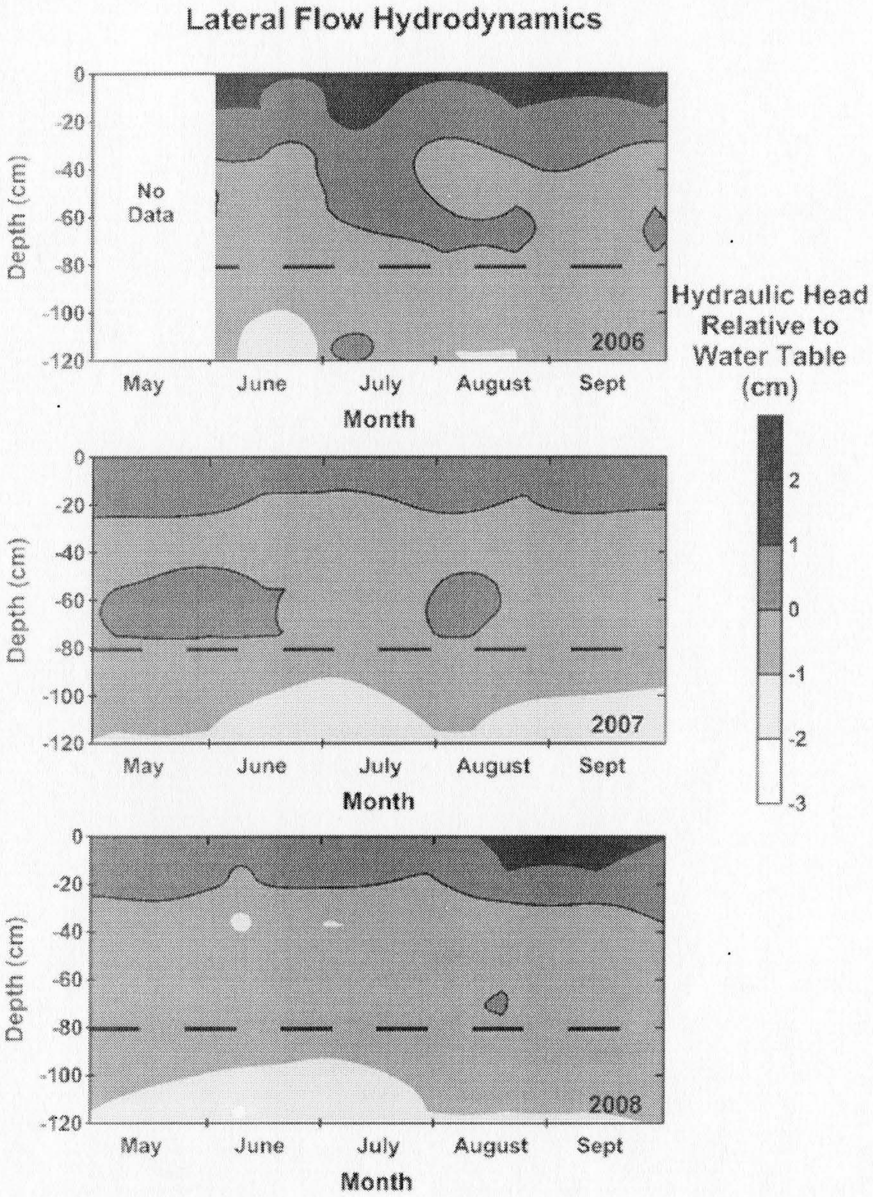

Figure 2.5: Representative seasonal hydraulic head relative to water table profiles through the peat and soil for the Lateral Flow Class. The dashed line in each plot represents the depth of the peat layer at the nest depicted. The solid black line represents the equipotential with the water table, separating the transition from overpressure heads (dark) to underpressure heads (light).

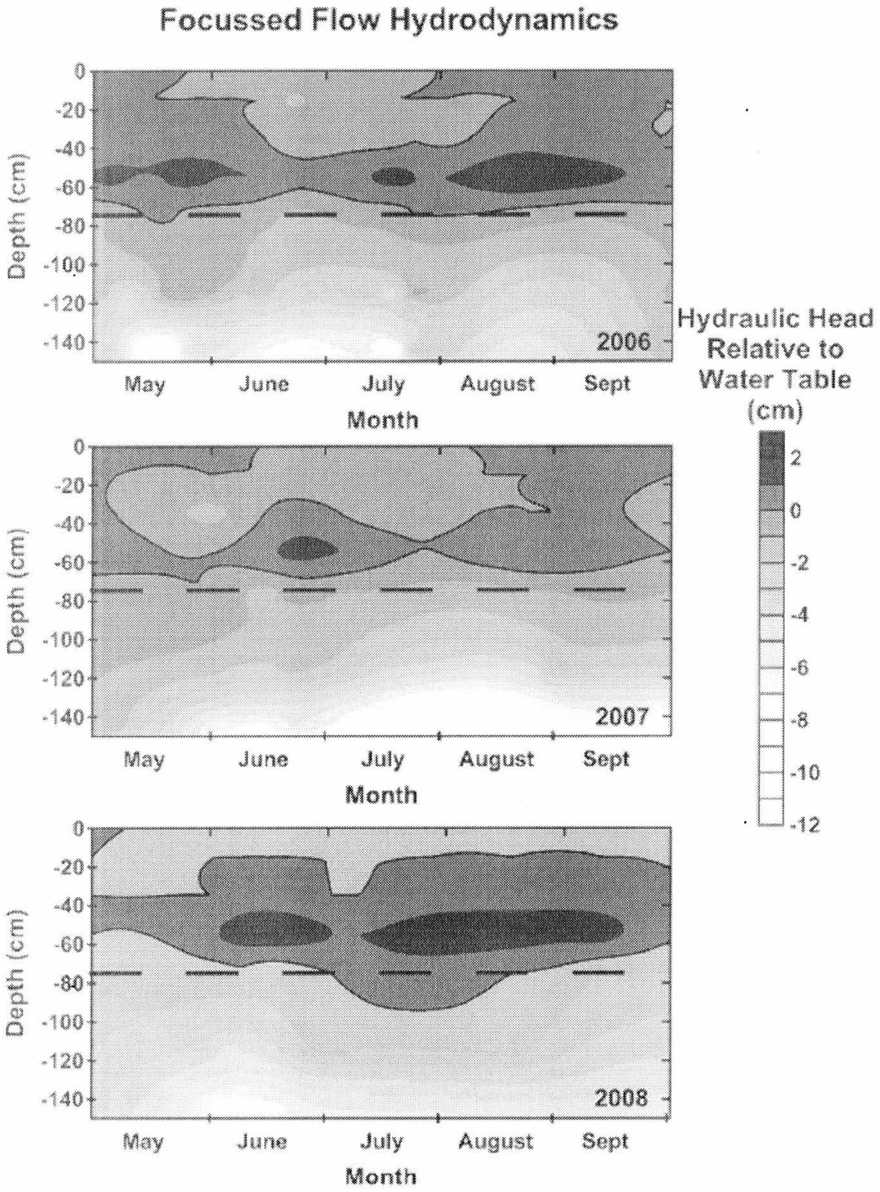

Figure 2.6: Representative seasonal hydraulic head relative to water table profiles through the peat and soil for the Focussed Flow Class. The dashed line in each plot represents the depth of the peat layer at the nest depicted. The solid black line represents the equipotential with the water table, separating the transition from overpressure heads (dark) to underpressure heads (light).

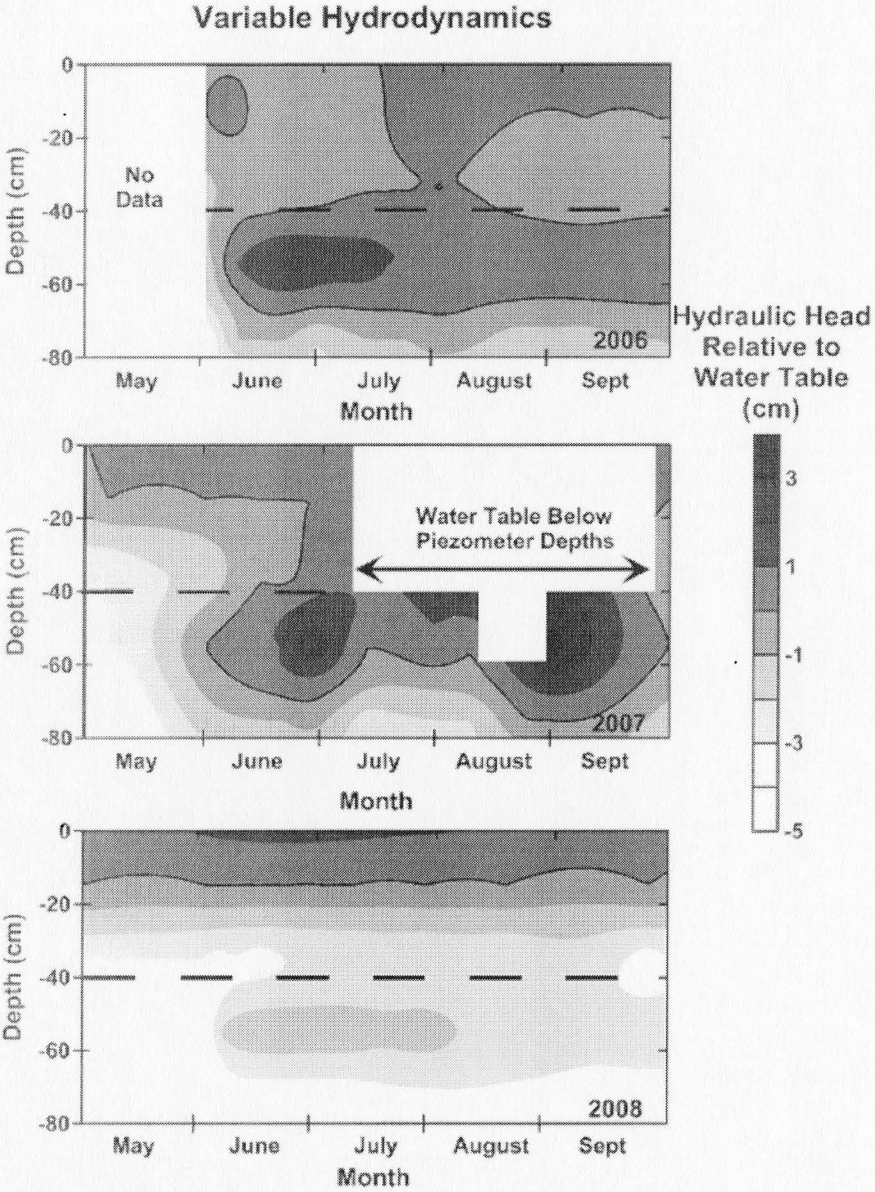

Figure 2.7: Representative seasonal hydraulic head relative to water table profiles through the peat and soil for the areas that change classification in response to interannual variability in precipitation. The dashed line in each plot represents the depth of the peat layer at the nest depicted. The solid black line represents the equipotential with the water table, separating the transition from overpressure heads (dark) to underpressure heads (light).

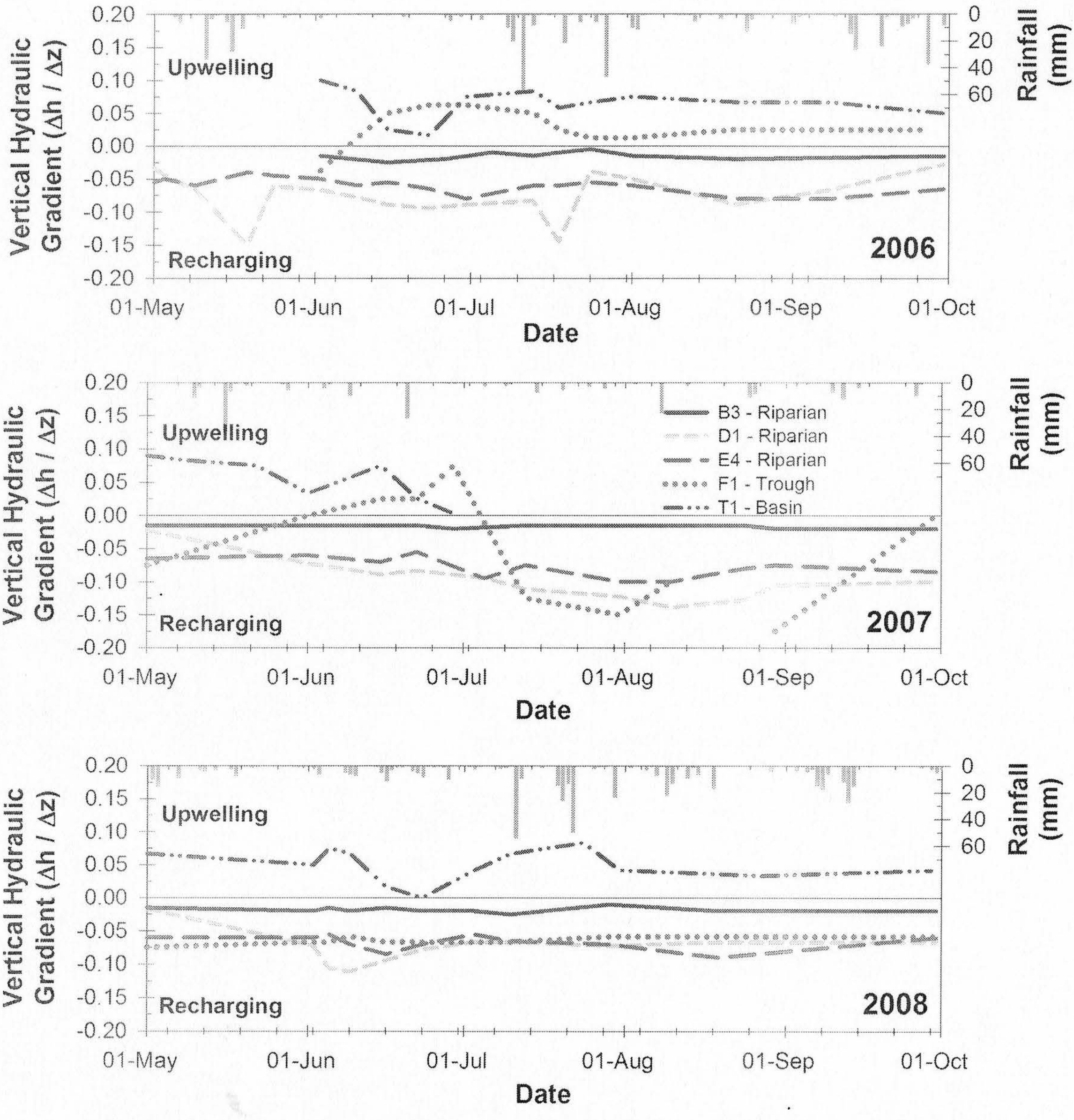

Figure 2.8: Seasonal variation in vertical hydraulic gradient for the piezometer nests depicted in Figures 2.3 to 2.7 representative of all nests.

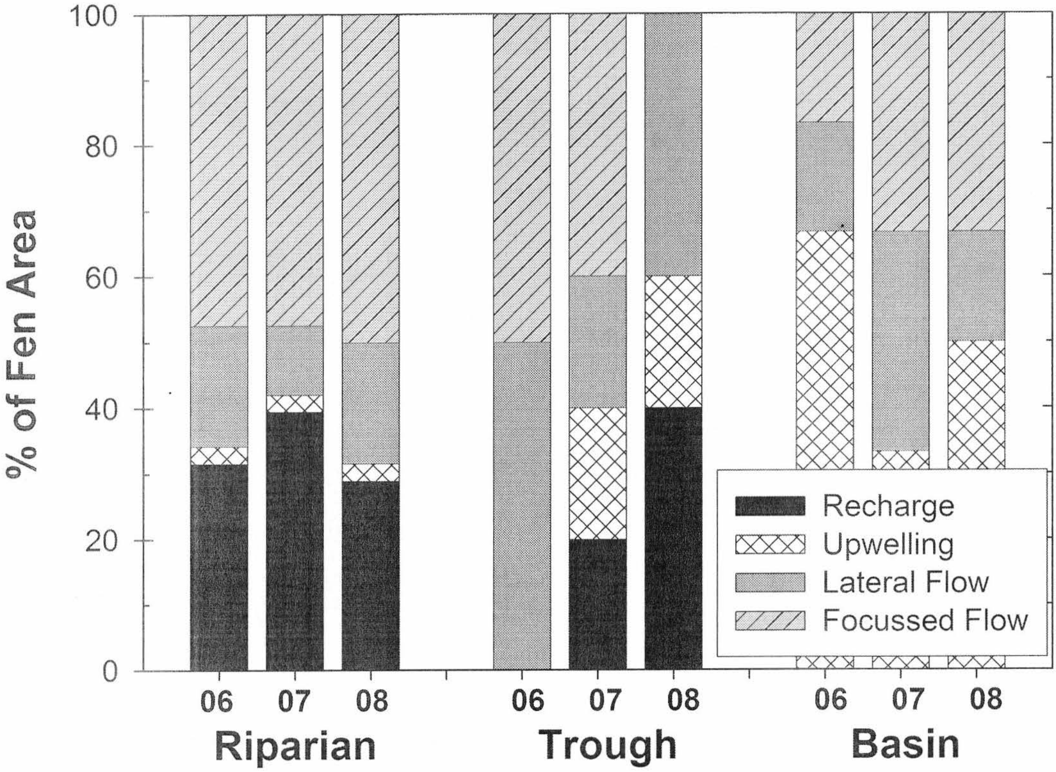

Figure 2.9: Interannual variability in calcareous fen hydrodynamic classification.

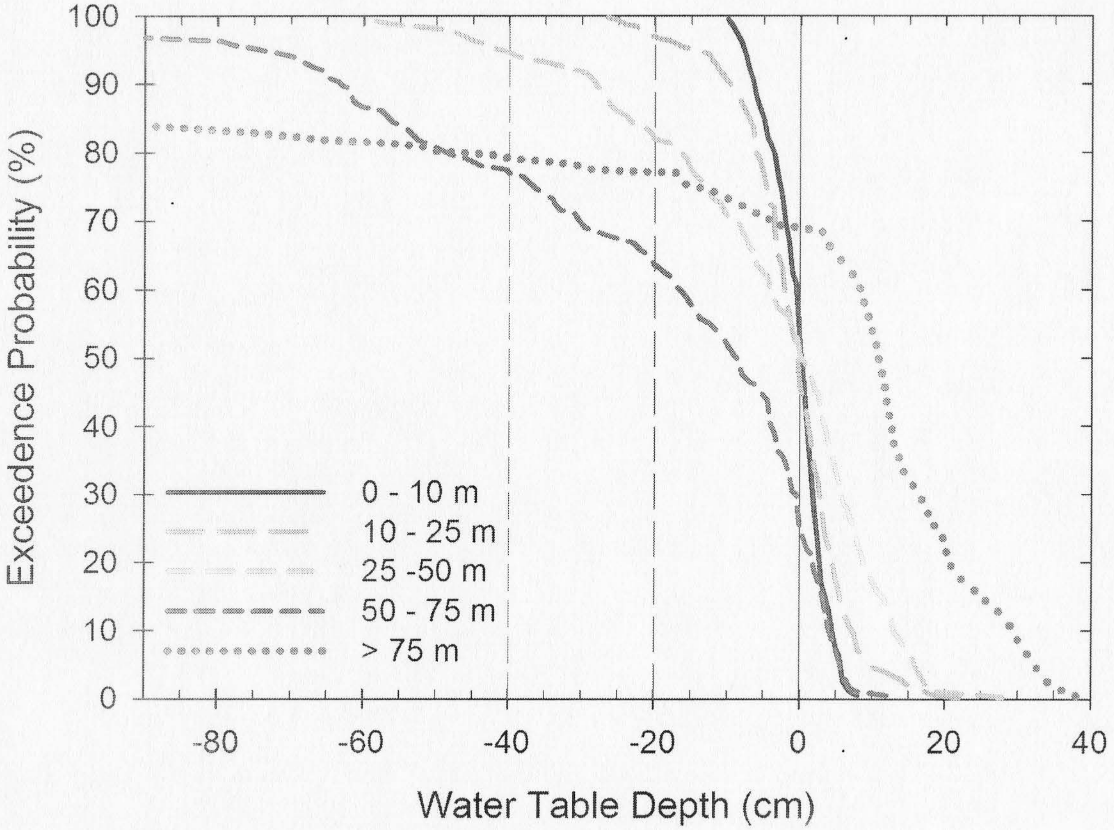

Figure 2.10: Exceedance probabilities of water table position of piezometer nests grouped by distance from Fletcher Creek.

CHAPTER 3:
HYDROGEOMORPHIC SETTING CONTROLS CALCAREOUS FEN WATER BALANCE AND FLOWPATHS

3.1 Abstract

Calcareous fens are species-rich peatlands that are dependent on minerotrophic water sources for wetland functioning and current conceptual models suggest the water source is ubiquitously groundwater upwelling. Here, we present evidence that calcareous fens can receive significant water from varied water sources dependant on their position in the landscape. The water balance and subsurface water flowpaths and fluxes were quantified for three calcareous fens differing in hydrogeomorphic setting over three growing seasons of vastly different precipitation inputs. The Riparian Fen received an order of magnitude more water than the Trough or Basin Fens. The Riparian Fen was dominated by stream recharge inputs and groundwater outputs. Precipitation and evaporation dominated the water balance of the Trough Fen. Only the Basin Fen received significant groundwater inputs. Variations in growing season precipitation led to subsurface flow reversals in all three fens. Subsurface water fluxes were low and groundwater did not travel appreciable distances within a growing season, due to weak hydraulic gradients and low saturated hydraulic conductivity in places. These results demonstrate the importance of landscape position, or hydrogeomorphic setting, in the hydrology of calcareous fens, and will aid in conservation, management, and restoration efforts of these important ecosystems.

3.2 Introduction

Calcareous fens are wetlands fed principally by water rich in calcium, magnesium, and bicarbonate (Komor, 1994; Almendinger and Leete, 1998b), have accumulated more than 40 cm of peat (National Wetlands Working Group, 1997; Mitsch and Gosselink, 2007), with near-surface soil and surface water pH in the range of 6.0 to 7.8 (Eggers and Reed, 1987; Bedford and Godwin, 2003). Dominated by sedges and brown mosses, calcareous fens exhibit very high vascular and non-vascular vegetation species richness and diversity (Motzkin, 1994; Johnson and Steingraeber, 2003), and serve as regional refugia for a number of rare plant taxa (Nekola, 1994; Bowles et al., 2005). They are also home to several endangered and regionally rare animal species, particularly amphibian, reptile, and insect species (Bedford and Godwin, 2003). As such, calcareous fens are key conservation and restoration targets in North America (Cooper and MacDonald, 2000; Amon et al., 2002) and Europe (Jansen et al., 1996; Lamers et al., 2002; Middleton et al., 2006). Despite the very high biodiversity value of these wetland ecosystems, little research has been conducted on the underlying hydrological processes controlling calcareous fen ecosystem development.

Synonymous with extreme-rich fens (Vitt and Chee, 1990; Zoltai and Vitt, 1995; Cooper, 1996), it is widely accepted that these peatlands require source water to flow through calcareous substrate, with the underlying geologic strata being either consolidated carbonate sedimentary bedrock (limestone or dolostone) or unconsolidated glacially deposited materials. The mechanisms by which that water enters the calcareous fen have received less attention. Based on limited empirical evidence, the base assumption is that upward hydraulic gradients prevail in the majority of the fen area; thus, settings conducive to groundwater discharge are necessary for calcareous fen formation (Gilvear et al., 1992; Almendinger and Leete, 1998b). Owing to the apparent requirement of alkaline groundwater discharge, conceptualization of calcareous fen formation and maintenance has been undertaken from a hydrogeologic setting framework, where the principal source area of calcareous water is assumed to be groundwater seepage points within the fen (Amon et al., 2002). However, several studies on calcareous fens report varying landscape position and connection to surface water (Koerselman et al., 1990; McNamara et al., 1992; Komor, 1994; Drexler et al., 1999a; Godwin et al., 2002; Boomer and Bedford, 2008). This suggests that hydrogeomorphic setting is also important in regulating calcareous fen function and hydrological processing.

The hydrogeomorphic setting (HGM) of a wetland refers to its geomorphic position in the landscape (ex. riparian, depressional, lacustrine), which imparts controls on the relative sources of water (precipitation, groundwater, surface water) to a wetland and their inherent hydrodynamic energies (Brinson, 1993). This approach is frequently adopted for wetland classification and assessment of hydrologic, biogeochemical, and ecological functions, largely in a regulatory context (Smith et al., 1995; Cole and Brooks, 2000a, 2000b; Gilbert et al., 2006; Hill et al., 2006). Hydrogeomorphic setting is a strong control on the hydrology and soil environment, which in turn controls the vegetation composition (Rheinhardt, 2007; Mitsch and Gosselink, 2007). Therefore, greater appreciation of the role of hydrogeomorphic setting on calcareous fen hydrology will enhance our understanding of fen functioning.

Previous research suggests calcareous fen species diversity (this wetland type's most important function) is tightly linked to hydrologic regime, through hydrogeologic settings promoting groundwater discharge, yet different fens of similar hydrogeologic setting display vastly different species diversity dynamics (Vitt and Chee, 1990; Nekola, 2004; Hájková et al., 2004; Locky and Bayley, 2006; Grootjans et al., 2006). The influence of hydrogeomorphology in the dynamics of hydrologic regime and its influence on calcareous fen function have received only cursory attention. Additionally, there exist only a few detailed hydrologic studies of calcareous fens (but see Drexler et al. (1999a, 1999b) and Drexler and Bedford (2002) for one New York calcareous fen). This lack of hydrological information and failure to document the influence of hydrogeomorphology on calcareous fen dynamics makes it difficult to develop process-based conceptualization of calcareous fen function that would improve conservation and restoration strategies.

Here we determine the role of hydrogeomorphic setting on the hydrology of calcareous fens contained within a single hydrogeologic setting: an area of regional groundwater recharge. By studying fens within the same hydrogeologic setting we can more accurately assess the influence of landscape position on calcareous fen hydrology. Specifically our objectives were to answer the following questions: (1) What are the magnitudes of the components of the growing season water balances of fens of different hydrogeomorphic setting? (2) How does hydrogeomorphic setting control the variability of water flowpaths and fluxes within these sites? And (3) how do the water balances, flowpaths, and fluxes vary between three growing seasons of varying climate conditions?

Results from this work will be valuable in conservation and restoration efforts through formulation of more informed generalizations that will aid in ecosystem management decisions.

3.3 Study Area

The three calcareous fens are located in a 332 ha headwater catchment of the Spencer Creek Watershed, 70 km west of Toronto, Ontario, Canada (43° 24' 57" N, 80° 7' 3" W). The catchment spans 50 m of elevation, from 337 to 287 m above sea level and is underlain by fractured dolomite of the Guelph Formation (Upper Silurian in age). The northern half of the catchment contains 0 – 25 m of glacial till derived from the Galt Moraine northwest of the catchment. The till grades into outwash fine sands and silts at the northern boundary of the fens. The southern half of the catchment contains no glacial overburden and soils range from 0 – 60 cm thick. Upland vegetation consists primarily of *Thuja occidentalis* L. (eastern white cedar) and *Betula papyrifera* Marsh. (paper birch) thicket interspersed by grass and shrubland. A series of groundwater seeps emerge mid-way down the catchment, which coalesce in a cedar swamp to form a clear, cold-water stream. This stream, Fletcher Creek, then flows through one of the calcareous fens, followed by a cedar swamp, then a cattail marsh at the outlet of the catchment. Historically, much of the glacial drift was excavated for gravel aggregate, resulting in steep hills in sections. Present land-use is a mixture of pasture and very low density residential.

For ease of comparison the unnamed fens are designated by their hydrogeomorphic position, using the nomenclature of Brinson (1993) and Godwin et al. (2002). At 4.5 ha the largest calcareous fen in the catchment is the Riparian Fen. It is bounded to the southwest by cedar swamp, the southeast and east by forested upland, the north by a railway, and the west by a county road. The Riparian Fen is gently sloping, with only 30 cm elevation change across 450 m of stream length (stream gradient of 0.00067). Vegetation of this site is variable, with the western half a mixture of fen sedges (*Carex flava* L., *C. livida* (Wahlenb.) Willd., *Rhynchospora alba* (L.) Vahl) and shrubs (*Rhamnus alnifolia* L'Hér., *Cornus stolonifera* Michx., *Rubus pubescens* Raf.), with the isolated areas of *Thuja occidentalis* L. and *Larix laricina* (Du Roi) K. Koch trees. The eastern half is primarily sedge-dominated (*Carex aquatilis* Wahlenb., *C. prairea* Dewey ex Alph. Wood, *C. livida* (Wahlenb.) Willd.) with areas of *Menyanthes trifoliata* L., *Scirpus acutus* Muhl., and *Lysimachia thyrsiflora* L. co-dominance. A small pool occupies the southern-most portion, which is surrounded by calcite precipitate known as a marl flat (Miner and Ketterling, 2005).

The intermediate-sized fen is a Trough Fen. This long, thin 2 ha fen is bordered on the east by an upland thicket of cedar trees, to the north by the railway, which separates the fen from a marl-accumulating pond to the north, and to the west and south by a riparian cedar swamp. The minimum distance from the edge of the Trough Fen to Fletcher Creek is 20 m at points at the northernmost, middle, and southernmost portions of the fen. Elsewhere, the fen is separated from the stream by 40-75 m of riparian swamp. Vegetation in the Trough Fen is generally sedge-dominated (*Carex lacustris* Willd., *C. stricta* Lam., *C. lasiocarpa* Ehrh.) with co-dominance of grasses (*Calamagrostis* *canadensis* (Michx.) P. Beauv.) to the north, herbaceous species (*Eupatorium maculatum* L., *Lycopus uniflorus* Michx.) in the middle-north, rushes (*Juncus canadensis* J. Gay ex Laharpe) in the middle-south, and cattails (*Typha angustifolia* L.) in the south. There is 43 cm of elevation change along the 200 m length of the wetland.

The smallest wetland studied was the Basin Fen. It was only 0.45 ha is size, and occupies a gentle depression in the upland cedar forest. There is at least 100 m of cedar upland or cedar swamp between the Basin Fen and Fletcher Creek, with no surface connection. The vegetation of the Basin Fen is sedge-dominated (*Carex stricta* Lam., *Carex utriculata* Boott, *Dulichium arundinaceum* (L.) Britton) with co-dominance of willow shrubs (*Salix pedicellaris* Pursh, *S. petiolaris* Sm.). Elevation of the fen floor varied by only 15 cm; however, the formation of tussocks of peat up to 70 cm above this fen floor by Upright Sedge (*C. stricta*) led to a highly variable surface topography.

3.4 Methods

3.4.1 Hydrometric Measurements

To monitor hydraulic head and water table position a series of piezometer nests were installed at each of the sites (Figure 3.1). Piezometers were constructed of 2.5 cm ID PVC piping with the bottom 10 cm slotted with 0.5 cm diameter perforations. The slot zone was screened with 250-μm diameter NITEX mesh. Piezometers were installed by auguring a hole to the desired depth using a 1-inch diameter soil auger and hammering in the piezometers. Each nest of piezometers consisted of four to six piezometers at nominal depths of 20, 40, 60, 80, 120, and 150 cm (depth reflects bottom of the slot zone). At some nest locations bedrock was reached prior to 120 cm depth; in those locations only the upper four piezometers could be installed. Each nest included at least one piezometer below the depth of peat into the mineral substratum. Wells were installed similar to the piezometers, and had perforations slotted throughout the peat profile and into the mineral substrate. Hydraulic heads and water table depths were recorded approximately weekly during three growing seasons (May-September 2006-2008). Saturated hydraulic conductivity (K_{sat}) of the peat and underlying mineral substrate was determined in each piezometer using the Hvorslev bail technique (Freeze and Cherry, 1979). Flow nets were determined using interpolation software (Golden Software, 1999). Subsurface water fluxes were calculated assuming steady state and isotropic conditions following Darcy's Law (Freeze and Cherry, 1979).

Meteorological measurements were made at a station in the eastern portion of the Riparian Fen. A tipping bucket rain gauge connected to a Campbell Scientific CR10X data logger recorded rainfall during the measurement period. Potential evapotranspiration was estimated using the Priestley-Taylor approach (Oke, 1972). A Kipp and Zonen NR-Lite was used to measure net radiation (Q^*) at 1.5 m above ground surface, and two REBS HFT3 soil heat flux plates inserted to 5 cm depth were used to determine ground heat flux (Q_g). Air temperature was recorded using a Campbell Scientific 107 Thermistor in a radiation shield.

Stream discharge through the Riparian Fen was recorded at the inlet and outlet to the fen using proper stream currenting technique (Carter and Davidian, 1968). Continuous (20-min interval) measurements of stream stage were made using pressure transducers (Solinst Levellogger Golds) immediately upstream of a 1-m diameter culvert under the county road as water entered the fen and immediately downstream of a built flume (1 m X 1 m flow area) at the outlet to the fen. Because of the presence of fish and turtles, weirs could not be used. The culvert and flume were used as gauging stations. Discharge (Q) measurements were made at least monthly using a 2-D Acoustic Doppler Velocimeter (SonTek). Rating curves were developed relating instantaneous discharge to continuous stage for each year of study. All rating curves had an $r^2 > 0.95$, with most seasonal rating curves > 0.97.

3.4.2 Water Balance

An estimate of growing season water balance for each of the sites was made for each year of study. The water balance for each fen was calculated as follows:

$$P - ET + R_{in} - R_{out} + GW_{in} - GW_{out} = \Delta S + \varepsilon, \qquad [1]$$

where P represents precipitation, ET evapotranspiration, R_{in} and R_{out} the streamflow entering and leaving the site respectively, GW_{in} and GW_{out} the groundwater entering and leaving the site respectively, ΔS the change in storage of water in the fen, and ε the residual. Precipitation was measured as above at the Riparian Fen site and assumed to not differ over the ~500 m between sites.

To relate potential evapotranspiration as determined above to actual evapotranspiration an α value of 1.26 was used for fen surfaces that were well watered (Priestley and Taylor, 1972; Rouse and Stewart, 1972). During several intervals in the measurement period the water table fell well below the ground surface (> 40 cm) in the Basin Fen, the middle portion of the Trough Fen and the north-central portion of the Riparian fen. During these time intervals the wetland surface can no longer be considered well watered; as such, the use of an α coefficient of 1.26 is invalid. While attempts to relate PET to AET in this study were not fruitful, and to the best of our knowledge there are no other studies documenting an α value for fens subject to large water table drawdown, based on a review of the pertinent literature (Wever et al., 2002; Gavin and Agnew, 2004; Burba and Verma, 2005; Pauwels and Samson, 2006; Petrone et al., 2006; Sun and Sang, 2008) an α coefficient of 0.8 was used for the areas and during the periods for which the water table was at least 20 cm below the surface. For these time intervals, the evapotranspiration value for each site was weighted by area for regions of differing AET/PET. The area of the stream of the Riparian Fen was assumed to evaporate at the same rate as the wet fen surfaces.

Streamflow entering and leaving the Riparian Fen was based on daily averages of calculated discharges. Groundwater inputs and recharge were calculated based on the hydraulic gradients from the weekly hydraulic head measurements and the hydraulic conductivity determinations from each piezometer nest. Weekly groundwater changes for each nest were assumed to be a representative value for the surrounding peat.

The change in storage term was calculated based on water table fluctuation and measures of specific yield. We determined specific yield on representative samples from each vegetation community post hoc; that is, specific yield measurements were made on soil cores to a depth subject to water table decline for each area. Determination was made in 5 cm intervals on cores 10 cm in diameter. Soil cores were withdrawn from the fens using 10 cm diameter ABS pipe. There was < 2 cm compaction of 80 cm cores using this technique in these fens. Cores were frozen until analysis, whereupon they were sectioned, weighed, allowed to saturate in water for 3-5 days, re-weighed, covered in plastic sheeting and allowed to drain for 24 hours, re-weighed again. Specific yield was calculated as:

$$S_y = \frac{(M_S - M_D)/\rho_W}{M_S/\rho_W}, \qquad [2]$$

where S_y ($m^3\ m^{-3}$) represents the specific yield (≤ porosity), M_s is the saturated weight of the sample, M_D is the weight of the sample after it was allowed to drain and ρ_W is the density of water, assumed to be 1 g cm^{-3}.

3.4.3 Error Analysis

The residual in the water balance calculation is a lumped term that represents the error in measurement techniques as well as any additional water inputs, outputs, or storage that we were unable to measure. Error in the precipitation measurement was assumed to be ±10 % (Winter, 1981). Assuming Q* was accurate to within 10 %, Q_g to within 20 %, and because Q* was much larger than Q_g, evapotranspiration using the Priestley-Taylor approach was assumed to be ±20 % (Angus and Watts, 1984; Price, 1996). Error in stream discharge is comprised of errors in stage measurement, velocity measurement, and the stage-discharge relationship. Over the range of stage fluctuation the pressure transducers were accurate to ±3.5 mm, or ~2 %. The velocimeter was accurate to 1 % of each measurement and very good stream currenting technique was used; therefore, discharge error was assessed at ±5 %. Using the correlation of the stage-discharge model, streamflow error at each station was calculated to be ±30-40 %, depending on the year and station, which is in line with other estimates (Owen, 1996). Groundwater estimates are subject to large errors in the assumptions implicit in the hydraulic conductivity measurements and are difficult to assess; however, previous research has ascribed an uncertainty in these estimates as ±100 % (Koerselman, 1989; Drexler et al., 1999a).

3.5 Results

3.5.1 Calcareous Fen Hydrophysical Properties

The saturated hydraulic conductivity varied within and between the calcareous fens. Figure 3.2(a) depicts representative hydraulic conductivity profiles with depth in the calcareous fen peat and mineral substrate. Hydraulic conductivity generally decreased with depth across one order of magnitude in some nest locations (D4) to as much as five orders of magnitude in others (C1), with surficial peat being significantly more conductive than deeper peat and underlying mineral substrate (Table 3.1; Kruskal-Wallis test statistic = 25.251, p-value = 0.00012). K_{sat} was significantly higher (Kruskal-Wallis test statistic = 11.125, p-value = 0.004) in the Riparian Fen (geometric mean 5.13 X 10^{-4} cm s^{-1}) than the Trough Fen (4.88 X 10^{-5} cm s^{-1}), which was significantly higher than the Basin Fen (9.35 X 10^{-6} cm s^{-1}; Table 3.1). Overall, the peat was more conductive than the underlying mineral substrate (Mann-Whitney U test statistic = 509, p-value = 0.002), with a geometric mean one order of magnitude higher (10^{-4} vs. 10^{-5} cm s^{-1}). There were discrepancies to this general trend however, as the fine sands at 120 and 150 cm deep near the stream at piezometer nest A3 were more conductive than the overlying peat at 60 and 80 cm deep (Figure 3.2a). There was also a layer of fine silt at ~ 95 – 130 cm deep around piezometer nests B1, C1, and C2 that had very low hydraulic conductivities of 10^{-6} cm s^{-1}; these were an order of magnitude lower than the overlying peat or underlying fine sands (Figure 3.2a).

There was no clear spatial pattern of the peat specific yield among or between the calcareous fens. In general, S_y was greatest in the surface peat and decreased with depth (Figure 3.2b). In some cases this was a marked decrease, from values ~0.3 within the top 5 cm of the peat to 0.1-0.2 at 5-10 cm depth, averaging 0.075 for the remainder of the peat profile. In other cases, the decrease from the upper 5 cm was less pronounced: from 0.15 to 0.1, before reaching the average value of 0.075 at greater depths. The sedge tussock material of the Basin Fen and the very south area of the Trough Fen appeared to have a greater water retention capability, with specific yields >0.25 throughout their extent; this was in contrast to the Basin Fen subsurface peat, where all samples were <0.15.

Only the Riparian Fen was consistently influenced by the second-order Fletcher Creek. The stream was strongly influenced by year-to-year precipitation, as mean daily discharge values into the fen of 84.0, 72.8, and 117.4 L s^{-1} in 2006, 2007, and 2008, respectively (Table 3.2), were in-line with growing season precipitation variation (normal, dry, and wet years, respectively, Chapter 2). The range in stream discharge entering the fen was greater in 2006 and 2008 (max Q of 251.8 and 237.8, min Q of 56.6 and 46.8 L s^{-1}; respectively) than the dry 2007 growing season, where discharge peaked at just 127.6 L s^{-1}, with a low of 45.1 L s^{-1}. Figure 3.3 reveals that the Riparian Fen served as a strong losing stream reach of Fletcher Creek, averaging a loss of water through the fen of 31.1, 18.2, and 24.7 L s^{-1} in 2006, 2007, and 2008, respectively (Table 3.2). Excluding a possible error following the start of stream stage measurements in late May 2006, the daily average loss of stream flow through the Riparian Fen remained stable through 2006, with a coefficient of variation of 0.31. During the dry 2007 growing season, however, there was a noticeable and progressive decrease in the amount of stream flow being retained in the fen, as both discharge in and out of the fen decreased. In the extremely wet growing season of 2008, peak discharge occurred much later in the season, and the amount retained in the fen was quite variable (Figure 3.3), ranging from daily average maximums of 53.2 L s^{-1} to the stream becoming a gaining reach of 3 L s^{-1} in September 2008.

3.5.2 Water Balance

The large retention of stream flow in the Riparian Fen became the dominant component of that fen's water budget for all three growing seasons (Figure 3.4a). In 2006 the slope of this addition of water to the fen remained constant throughout the growing season, whereas the slope continued to decrease throughout the dry 2007 growing season, and fluctuated throughout the wet 2008 season. The greatest outlet of water from the Riparian Fen was groundwater recharge, which was more than twice the loss due to evapotranspiration. The vast majority of this groundwater recharge was concentrated in and around the area of piezometer nests D4 and E4 and the pool at the southern-most portions of the fen (Figure 3.1). The groundwater recharge of ~1200 mm was consistent between years. Groundwater discharge into the Riparian Fen was negligible (< 50 mm). The very large difference in stream flow in and out of the fen resulted in a very large depth of water that could not be accounted for by the water balance equation.

Inputs to the Trough and Basin Fens were dominated by precipitation (Figure 3.4b and c). Both groundwater in and out were minor components of the water balance of the Trough Fen in all three growing seasons (< 50 mm). A dry June 2006 created a significant P-ET water deficit in the Trough Fen; however, the water table (change in storage) did not drop appreciably during this period, leading to an increased negative residual of unaccounted for water. Increased summer precipitation helped offset the evaporative demand, and the residual was a modest -28 mm (Table 3.3) at the end of the 2006 growing season in the Trough Fen, in addition to a measured water deficit of 43 mm (Table 3.3). In 2007 the very low precipitation was less than half the evaporative demand, leading to a decrease in fen water storage through the early summer (Figure 3.4b). However, the measured decrease in storage was not as large as calculated from the other components; thus, the negative residual in the water balance equation continued to increase, reaching a sizeable -292 mm at the end of the growing season. This large negative residual suggests that there clearly was an unaccounted input of water to the system. The 2008 water balance of the Trough Fen was characterized by early-season moderate precipitation inputs leading to a decrease in storage and residual (Figure 3.4b), followed by increased precipitation producing a surplus of water in the fen, which decreased through September to produce a small negative residual at the end of the growing season (Table 3.3).

The Basin Fen was the only studied fen with appreciable groundwater inputs, though these inputs were still < 50 % from precipitation (Figure 3.4a, Table 3.3). As long as there is sufficient upslope recharge this groundwater discharge in to the fen occurred at a near constant rate. In 2006 the combined inputs of groundwater discharge and rainfall kept pace with the evaporative demand in May, but low June precipitation led to a water storage deficit. Increased summer precipitation led to a closure of the water balance by the end of the growing season, with just a +10 mm residual. In May 2007 a large magnitude rainstorm without a proportional water table response resulted in a calculated positive residual in the Basin Fen (Figure 3.4c). This residual was progressively reduced throughout the growing season as the very large P-ET deficit of summer of 2007 resulted in the water table falling below the depth of our piezometers by the end of July (Figure 3.4c). That is, groundwater inputs sufficient to produce a water table (and be detected by our methodology) were stopped at 105 mm, as did changes to water storage in the form of a water table fluctuation, which was measured at -179 mm at the end of July 2008 (Table 3.3). With a lack of groundwater input, and no further changes to saturated fen water storage for August and September, the P-ET deficit reduced the positive residual from earlier in the growing season and closed the water budget, though there was no re-emergence of the water table until late October (data not shown). From May to mid-July 2008 the normal precipitation and groundwater inputs were sufficient to maintain the water table near the surface in response to slightly less evaporative demand (as temperatures were cooler). Record summer rainfall however, resulted in a greater storage in the fen, as well as a high positive residual (98 mm) of unaccounted for water (Figure 3.4c).

Assuming net radiation was similar between the location of our met station (Figure 3.1) and the three calcareous fens and that our α coefficients were valid, growing season evapotranspiration totals ranged from 510 to 616 mm between the fens and three different growing seasons (Table 3.3). In the normal 2006-growing season the Basin Fen maintained water tables within 20 cm of the surface for the entire season, whereas portions of the Riparian and Trough Fens did experience significant water table drawdown; thus, ET was 15 to 30 mm greater in the Basin Fen. However, in the dry 2007-growing season, the entire Basin Fen experienced severe water table drawdown, limiting ET to 40 mm less than the Trough Fen, and 100 mm less than the Riparian Fen, where the majority of the fen had a water table within 20 cm (Chapter 2). The very wet and cooler 2008-growing season resulted in water levels being above the -20 cm threshold at all three sites; thus, ET was calculated at 510 mm in each studied calcareous fen.

The three calcareous fens in close proximity to one another were subject to vastly different magnitudes and proportions of the growing season water balance components (Table 3.3). At between 5000 and 6800 mm, the input of water to the Riparian Fen was dominated by the dynamics of Fletcher Creek. Between 1100 and ~1400 mm of this water input was accounted for by diffuse groundwater recharge. In contrast, the Trough Fen was characterized principally by P-ET dynamics and only subject to less than 700 mm of total water inputs and outputs, an order of magnitude less than the Riparian Fen. Only the Basin Fen was dependent on a significant proportion of groundwater input, representing between 20 and 33 % of total inputs. These detected groundwater inputs resulted in the Basin Fen receiving slightly more water than the Trough Fen. The variable water balance magnitudes and proportions had important consequences for flow paths and fluxes of water within the three calcareous fens.

3.5.3 Subsurface Water Flow Paths

In the latter half of the 2006 growing season and nearly all of the wet 2008-growing season the Riparian Fen was either saturated or subject to water above the ground surface (Figure 3.5a). During these periods the dominant flow direction through the fen was parallel to Fletcher Creek, along the long axis of the site. The 30 cm decrease in the water table position across the fen during these periods was slightly less than the 40-cm drop in ground elevation (Figure 3.5c). During these wet periods there was a sustained hydraulic gradient from west to east into and through the fen peat that was mirrored in the subpeat sand layer (Figure 3.5a); however, the horizontal component to this hydraulic gradient was quite low (~0.001 from A2 to E1). Additionally, there was a persistent slight overpressuring of the water in the sand beneath the peat in the A2 nest.

In contrast to the along-fen flow path of the wet periods in the Riparian Fen, the direction of flow during the dry periods (first half of 2006 and all of 2007 growing seasons) was strongly perpendicular to Fletcher Creek (Figure 3.5d). That is, the stream became the dominant influence on subsurface water movement, as there was sustained stream recharge into the peat. The general hydraulic gradient direction between A2 and C2 remained the same as high water table times, but nearly tripled in magnitude (from 0.0005 during wet periods to 0.0013 during dry periods). The planform water table pattern resulted in a reversal of the groundwater flow direction between nests C2 and D1 relative to the wet periods (cf. Figure 3.5a & b). Thus, there was also a small ~0.0011 horizontal hydraulic gradient from the D1 nest towards the C2 nest. Areas of the Riparian Fen around the D and E transects were least affected by the drier portions of the study period, experiencing at most a 10 cm water table drawdown, whereas the B and C transects were subject to up to a 50 cm water table drawdown (Figure 3.5d; details in Chapter 2).

While the prevailing hydraulic gradient across the fen was downvalley during the wet periods, there was still evidence of stream recharge into the peat (Figure 3.6a). The stream becomes increasingly important as a water source to the A, B, and C transects during drier periods, and horizontal hydraulic gradients inland from the stream exceed 1.2 % (Figure 3.6b). Furthermore, the eastern portion of the fen, typified by transects D and E, was perennially strongly influenced by Fletcher Creek (Figure 3.6c). Regardless of precipitation totals this portion of the fen did not experience a water table drawdown of more than 14 cm, and hydraulic gradients were consistently directed from the stream and its distributaries into the peat and underlying sand and dolomite.

All but a slightly elevated ridge in the Trough Fen was inundated with water for the latter half of 2006 and most of 2008 (Figure 3.7a). During these wet periods the water table gradient followed the general surface topography and was directed north-south down the long axis of the fen (Figure 3.7b). The prevalent hydraulic gradient through the Trough Fen peat under saturated conditions was downvalley at 0.002 from F1 to F4, with little vertical change in hydraulic head within a nest (Figure 3.7a). Most of this downvalley hydraulic gradient was concentrated in the northern half of the fen, where the gradient was ~0.003 from F1 to F3. From F4 to F5 the gradient dropped to a very modest 0.0007; that is, the southern half of the fen under wet conditions was nearly equipotential.

The dry periods of the growing seasons brought about a flow reversal in the Trough Fen (Figure 3.7b, d). While the water table was ~30 cm lower than during wet periods in the northern half of the fen, it was only ~10 cm lower in the southern half (Figure 3.7d), with much of this area still being inundated (Figure 3.7b). Indeed, during the dry periods, the water table resided below the peat layer throughout much of the northern half of the fen. This water table drawdown-induced flow reversal doubled the hydraulic gradient from F1 to F3 to 0.006, relative to the wet periods. There was also a very strong hydraulic gradient of 0.01 from F4 to F3. The southern half of the fen, from F4 onwards, did not have a demonstrable hydraulic gradient (Figure 3.7b).

The Basin Fen was inundated with between 20 and 40 cm of water during the wet periods of the studied growing seasons. Based on the hydraulic head measurements, most of this water originated as groundwater upwelling under the north regions of the fen (Figure 3.8a). There was only an 8-cm hydraulic head difference detected across the transect piezometers, and vertical hydraulic gradients of 0.075 (Chapter 2) were an order of magnitude larger than the horizontal gradients of 0.002 (Figure 3.8a). There was a resultant very slight water table gradient across the fen as the water table was 2.5 cm lower in the south than the north (Figure 3.8c).

In the dry 2007 growing season the water table fell below the level of the dolomite bedrock by the end of July and did not return until November of that year (Chapter 2). This led to a drop in the water table of at least a metre relative to high conditions in wet years. Before this severe water table drawdown, there continued to be a positive vertical hydraulic gradient in the central portion of the fen, which radiated outwards away from this discharge point (Figure 3.8b). This increased the horizontal hydraulic gradient from T2 to T3 to 0.022 and reversed and increased the hydraulic gradient from T1 to T2 to -0.008 (Figure 3.8d).

3.5.4 Subsurface Water Fluxes

Subsurface water fluxes were estimated for the dominant flowpaths identified. Along the west-east axis of the Riparian Fen specific discharge was calculated using mean hydraulic conductivities through the peat to average 0.3 L m^{-2} day^{-1} from the A2 to the E1 piezometer nests during wet and normal growing seasons. Because of the localized low hydraulic head at the C2 nest, during the dry growing season this flux decreased to 0.25 L m^{-2} day^{-1}. At these fluxes water along this flowpath would only travel between 38 and 46 mm in a growing season.

A flux of -0.3 L m^{-2} day^{-1} was calculated from the near-stream B3 piezometer nest to the B1 nest during wet periods; that is, groundwater travelled towards the stream during this period. During wet periods, however, the specific discharge increased to 7 L m^{-2} day^{-1} throughout the peat profile. Thus, even during the extreme water table drawdown that created the large hydraulic gradient, water would travel 1.1 m along this flowpath during a growing season. The vertical component of the hydraulic gradient in the southern portion of the Riparian Fen allowed a recharge of fen subsurface water to the groundwater system of -66 and -69 L m^{-2} day^{-1} in the wet and dry periods, respectively.

Under normal and wet conditions, when the water table was within the peat, horizontal specific discharge from the F1 to the F3 nest averaged 7 L m^{-2} day^{-1}. This flux decreased to 3 L m^{-2} day^{-1} from F3 to F4. During the dry periods when a water table was present, but resided in the underlying sand layer in the northern half of the fen, horizontal groundwater flux averaged less than 0.1 L m^{-2} day^{-1} from F1 to F3. The flux was slightly higher, but opposite direction, from F3 to F4, averaging -0.5 L m^{-2} day^{-1}.

Groundwater discharge into the Basin Fen was calculated to range from 1 to 1.2 L m^{-2} day^{-1} during wet and dry growing periods, respectively (only including periods with water table above dolomite bedrock). The horizontal component of specific discharge in the fen was less than 0.2 L m^{-2} day^{-1} during the wet periods, mostly due to the low hydraulic gradient, and less than 0.1 L m^{-2} day^{-1} during the dry periods, mostly due to the low hydraulic conductivities.

3.6. Discussion

3.6.1 Water Balance Closure

Our water balance model study failed to account for appreciable amounts of water at all sites (Table 3.3, Figure 3.4). Most notably, over 3000 mm of water was calculated to enter the Riparian Fen in a growing season, without any detected outlets. In late September 2007, during a very low stream discharge period water was observed to pour into several sinkholes into the bedrock located around the eastern most end of the fen (labelled in Figure 3.1). These sinkholes appeared to be in association with evidence of treefall, and probably were created by dissolution of the underlying dolomite by the organic acids of the fen peat followed by crevice expansion by the tree root anchors (Ford and Williams, 2007). Indeed, organic acid dissolution of the calcareous bedrock probably explains the diffuse large negative vertical hydraulic gradient and groundwater recharge throughout much of the fen.

The northern-most sinkhole was approximately 30 cm in diameter; the other three were 15-20 cm in diameter. Attempts to gauge stream recharge into these sinkholes in both 2007 and 2008 were moderately successful, with estimates of 5-12 L s^{-1} in the northern one, and 3-7 L s^{-1} in each of the other three. The lower ends of this range of recharge values were for 2007, when the recharge rate was lower than the capacitance of these crevices (which was the only reason they were detected in the first place). An average total recharge in to the bedrock system through these four point sources of 20 L s^{-1} equates to 5531 mm over the course of a growing season. This value is very close to the calculated residuals of 5600 and 5607 mm in the 2006 and 2008 water balance study years, and we suggest this is the process responsible for much of the unaccounted for excess water.

The stability of the change in streamflow in and out of the fen in 2006 from Figure 3.3 also supports the notion that so long as the stream is of a certain level a sustained and near constant amount of water re-enters the bedrock groundwater system at these sinkholes. The decreasing retention of streamwater in the fen in 2007 as stream stage and discharge continued to decrease (Figure 3.3) further explains the water balance for the Riparian Fen: the smaller residual (3355 mm) was indicative of lower stream recharge into the sinkholes as stream stage was too low to meet their maximum capacitance. In the wet 2008, when there was no consistent pattern to the change in streamflow, it was likely that there was still the constant ~20 L s^{-1} into the sinkholes, and the added detected retention in the fen was directed to surface storage within the fen (Figure 3.5a, 3.6a & c).

Another limitation to our water balance model was the inability to accurately account for changes in peat water storage in the unsaturated zone. For example, a 20 cm drop in the water table from the ground surface at the F1 piezometer nest withdraws only 45 mm of water from storage (based on calculated specific yields). However, with porosity of 0.85 in that layer, 125 mm of unsaturated water remains available. In the absence of further water table fluctuation it is assumed that this unsaturated water would contribute to plant transpiration. Thus, a sizeable portion of the large residual in the Trough Fen throughout 2007 (Figure 3.4b), for instance, was actually a decrease in unsaturated water storage, which explains why the residual so closely tracks evapotranspiration. There was approximately 325 mm of total unsaturated storage associated with an 80 cm water table drawdown in the central portions of the Trough Fen.

As the southern portion of the Trough Fen had a water table near the surface for all of 2006 and even most of the dry 2007, unsaturated zone storage changes alone cannot explain the resultant large negative residual (Table 3.3). At several locations along the western edge of the Trough Fen a diffuse, overland connection with the abutting riparian cedar swamp was observed. Because of the large errors associated with determining overland flow (Winter, 1981; Shaw and Prepas, 1990), as well as the dynamic nature of the stream-to-fen connection we did not include an estimate of this flowpath. However, there was geochemical as well as visual evidence that this connection did exist, as there was a progressive enrichment of chloride in the surface water of the Trough Fen downgradient (north-south) from 38 to 64.5 mg L^{-1}. This enrichment is indicative of mixing of high calcium-low chloride groundwater (93 and 38 mg L^{-1}, respectively; discharging at points such as F1) with high calcium-high chloride water (85 and 71 mg L^{-1}) from Fletcher Creek (Duval, unpublished data).

The surface water connection with the surrounding wetlands and uplands also aids in the explanation of the stable water table and close closure of the water balance of the Trough Fen in the wet 2008 growing season (Figure 3.4b, Table 3.3). The continued precipitation would be expected to significantly raise the water table of the fen, adding a surplus of water storage; however, with the onset of the large precipitation events from July 2008 until the end of the study period, the water table remained relatively stable (Chapter 2). We suggest that when the water table reached a critical threshold (~9-12 cm above ground surface in this fen) there was a sustained connection of surface flow out of the fen. Therefore, any additional water inputs, either through precipitation or overland flow from the elevated stream stage of Fletcher Creek, would runoff the fen at a faster rate than our measurement frequency.

The Basin Fen was the farthest from Fletcher Creek and thus, the least connected to a perennial water source. As such storage of water fluctuated the most within this fen, as dictated by variability in climate conditions. The small residual of 2007, even in response to continued ET demands, was most likely the result of continued unsaturated water withdrawal, as occurred with the Trough Fen. In 2008, however, there was nearly 100 mm of residual water that our model calculated. As this positive residual was sustained for the entire growing season, and the water table was above ground surface for all but a very small window, this discrepancy was either due to an overestimation of the groundwater inputs or a greater loss of water than we could account for. There was never a period of measurement in which there was detection of groundwater recharge beneath the peat (Chapter 2), and it seems unlikely groundwater inputs were significantly overestimated, as there was sustained upward vertical gradients throughout much of the fen and the calculated value was already less than the 2006 value (Table 3.3). Thus an additional outlet of water is the most likely result of this 100 mm of water. In 2008 standing water was frequently > 30 cm above the ground surface (Chapter 2). At this elevation the fen water is above the level of the surrounding uplands; therefore, the most likely explanation for the 100 mm of water is diffuse overland flow out of the fen into the surrounding cedar thicket. Indeed, very shallow surface water was detected along the southeastern perimeter of the fen for much of July-September 2008.

While many of the water balance components are subject to appreciable error in their measurement, the predominant trends within and between the fens are within these errors. Stream recharge is by far the dominant input to the Riparian Fen. It is possible, though unlikely, that diffuse groundwater recharge may have been of smaller magnitude than evapotranspiration in the Riparian Fen. The Trough Fen was clearly P-ET dominated, with no sustained stream inputs and very little groundwater inputs or outputs. The relative proportion of groundwater discharge and precipitation in the Basin Fen was the greatest relationship subject to the measurement error. If groundwater was underestimated by 100 % (capable while using physical theory of Darcy's Law) it is possible that groundwater discharge may have accounted for 50 % of the fen's water supply in all years, not the 20 to 30 % as measured in this study.

3.6.2 Calcareous Fen Subsurface Hydrology

All three calcareous fens were subject to a reversal of groundwater flow direction between the dry (2007) and wet (2008) growing seasons. While the occurrence of flow reversal is becoming increasingly widespread across a range of landscapes (Devito et al., 1997; Burt et al., 2002; Ferrone and Devito, 2004; Duval and Hill, 2006), directional change of groundwater flow path has usually been described within a single growing season, owing to increased evapotranspiration demands. It seems growing season drought is necessary to reverse flow direction in these calcareous fens; however, increased modification to the growing season weather patterns will be exacerbated by climate change, and could likely lead to greater drought conditions in these calcareous fens (Chapter 2). Greater likelihood of water table drawdown would paradoxically lead to greater rate of delivery of base-rich water to the fens. With the exception of the groundwater recharge under the marl flat of the Riparian Fen, the fluxes of groundwater in these calcareous fens are very low compared to previous work in other similar fens (Gilvear et al., 1993; Almendinger and Leete, 1998b), owing mostly to gentle hydraulic gradients, though low saturated hydraulic conductivity contributes to low fluxes. Hydraulic gradients increased in some cases by more than an order of magnitude with P-ET-induced water table drawdown. As the reversal of flow supplies more water from the base-rich stream to the Riparian and Trough Fens and the dolomite surrounding the Basin Fen, increases in specific discharge deliver comparatively more calcareous water than during high water summers. It is unclear how the trade-off between richer fen pore-water and lower water availability would affect calcareous fen ecosystem functioning.

3.6.3 Hydrogeomorphic Controls on Calcareous Fen Hydrology

All three of the study sites deviate significantly from the current conceptual model of calcareous fen functioning (Gilvear et al., 1993; Almendinger and Leete, 1998b). The Fletcher Creek wetland complex, which includes the three study fens, is situated within a groundwater recharge area. This hydrogeologic setting is not consistent with the framework of temperate zone fen formation put forth by Amon et al. (2002). Based on the framework methodology provided by Godwin et al. (2003) the three study fens were of the same chemical class, and differed in their spatial class (connectedness to surface water bodies), while it was not possible to estimate whether their physical attributes were similar enough to be of the same physical class; thus, it was not possible to relate our fens to the five groupings of that study. Regardless, the hydrological information presented here clearly demonstrates that the processing of water through these fens is fundamentally different from one another. Therefore, consideration of only hydrogeologic setting is insufficient for an accurate representation of fen functioning.

Landscape position, or hydrogeomorphic setting was the principal control on the delivery of water to and through the study fens. The Riparian Fen's connection to the second order stream dominated the water budget in all three growing seasons, and the backwater area of the marl flat allowed for stagnation of stream-derived water, which contributed to significant groundwater recharge. The Trough Fen was influenced by the stream, receiving ephemeral overland flow and subsurface contributions, but the magnitude of these components were less than that derived from precipitation and evapotranspiration. The Basin Fen, formed in a local depression in the landscape, was subject to appreciable groundwater discharge, but this component dried-up during the dry growing season, demonstrating that this groundwater source is local in origin, consistent with a regional recharge zone. However, chemically, while concentrations of dissolved solids differ (Chapter 4) between the fens, they all correspond to the extreme rich classification (Vitt and Chee, 1990; Eggers and Reed, 1997). Therefore, while none of the fens are directly connected to a regional groundwater discharge source, the interaction of their source waters with the underlying or surrounding geologic and sedimentary strata provides sufficient dissolution of carbonate minerals to supply the fens with base-rich water. For the Riparian Fen the stream is derived from a series of alkaline groundwater seeps; for the Trough Fen the mineral deposits beneath the shallow peat are very unconsolidated and calcareous; for the Basin Fen the surrounding uplands are all derived on dolomite and shallow calcareous soils.

These findings extend the conceptual model of calcareous fen formation in the temperate region by increasing the possible physical conditions capable of supporting active peat accumulation and calcicole plant success. Southern Ontario receives approximately the same magnitude of precipitation as the Midwestern USA where temperate fen concepts have been developed, but growing season evapotranspiration is slightly less (Amon et al., 2002), producing a greater surplus of water for fens than that region. It is possible that this water surplus may be the reason the study fens are capable of forming in this regional setting, without sustained groundwater discharge. At present, it is unknown how important regional climate variation is to calcareous fen formation. Further research in geographically different settings is required to determine how common are the conditions to support calcareous fen formation in non-groundwater discharge hydrogeologic settings.

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Table 3.1: Geometric Mean Summaries of Saturated Hydraulic Conductivity of the Calcareous Fens

	Hydraulic Conductivity (cm s^{-1})
Site	
Riparian	5.13×10^{-4}
Trough	4.88×10^{-5}
Basin	9.35×10^{-6}
Soil Type	
Peat	5.73×10^{-4}
Mineral	5.67×10^{-5}
Depth	
20 cm	6.34×10^{-3}
40 cm	3.57×10^{-4}
60 cm	1.31×10^{-4}
80 cm	2.52×10^{-5}
120 cm	1.81×10^{-4}
150 cm	1.61×10^{-4}

Table 3.2: Fletcher Creek Average Daily Discharge In and Out of the Riparian Fen for the Studied Growing Seasons (01-May – 30-Sept).

	R_{in}	R_{out} (L s^{-1})	ΔR
2006	84.0	52.9	31.1
2007	72.8	54.6	18.2
2008	117.4	112.6	24.7

Table 3.3: Water Balance Summaries at the Conclusion of the Studied Growing Seasons (01-May – 30-Sep) for Each Calcareous Fen.

Water Balance Components (mm)

Riparian Fen

	P	GW_{in}	ΔR	ET	GW_{out}	ΔS	ε
2006	481.5	37.8	6809.1	-584.4	-1150.3	-5.8	5599.5
2007	212.5	37.5	5045.5	-616.7	-1367.7	-43.5	3354.5
2008	549.5	38.4	6842.4	-510.0	-1270.7	42.5	5607.2

Trough Fen

	P	GW_{in}	ΔR	ET	GW_{out}	ΔS	ε
2006	481.5	34.3	~	-570.7	-15.8	-42.6	-28.1
2007	212.5	11.2	~	-558.7	-38.4	-81.1	-292.4
2008	549.5	0.3	~	-510.0	-45.5	31.9	-37.6

Basin Fen

	P	GW_{in}	ΔR	ET	GW_{out}	ΔS	ε
2006	481.5	226.9	~	-601.8	~	95.2	11.3
2007	212.5	105.2	~	-515.8	~	-179.4	-18.6
2008	549.5	144.9	~	-510.0	~	86.5	98.0

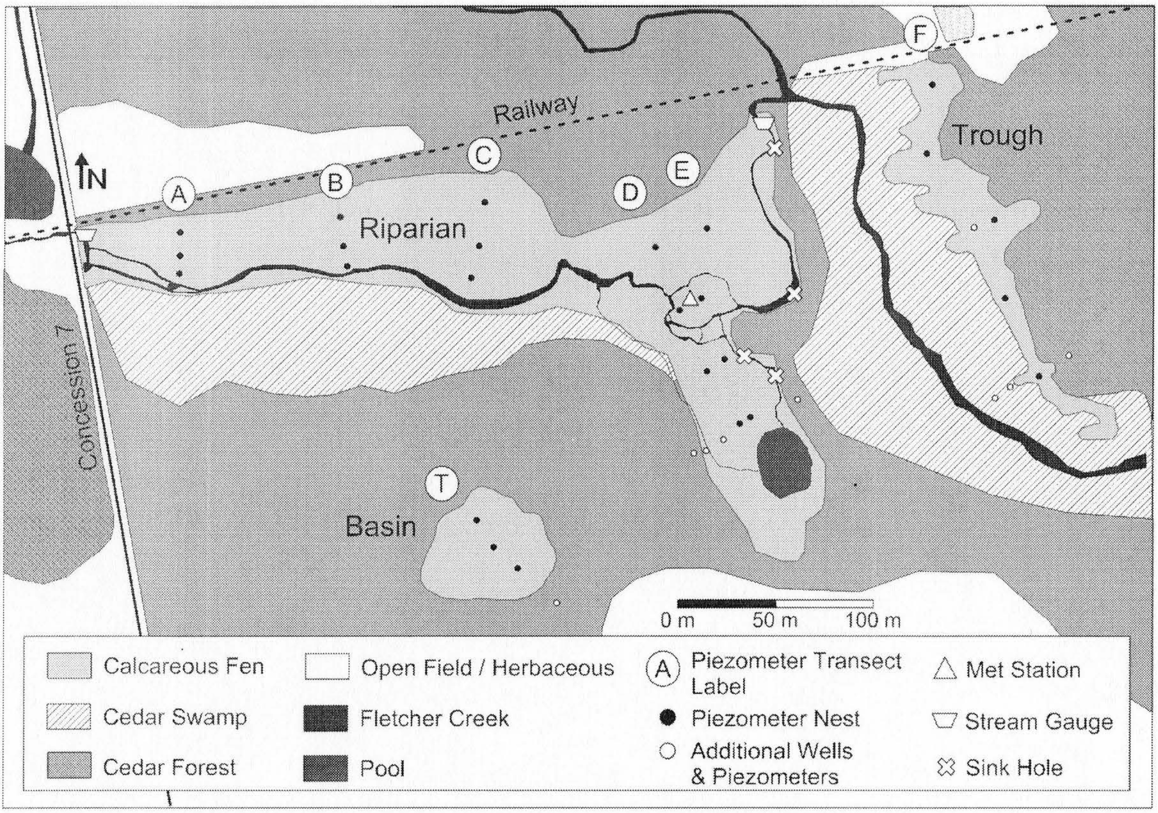


Figure 3.1: Map of a portion of the Fletcher Creek Ecological Preserve containing the three calcareous fens, indicating piezometer transects, stream gauging stations, and meteorological station. Piezometer nests are labelled alpha-numerically according to transect and incrementing position from the railway (e.g. piezometer nest A1 is the north-westernmost nest).

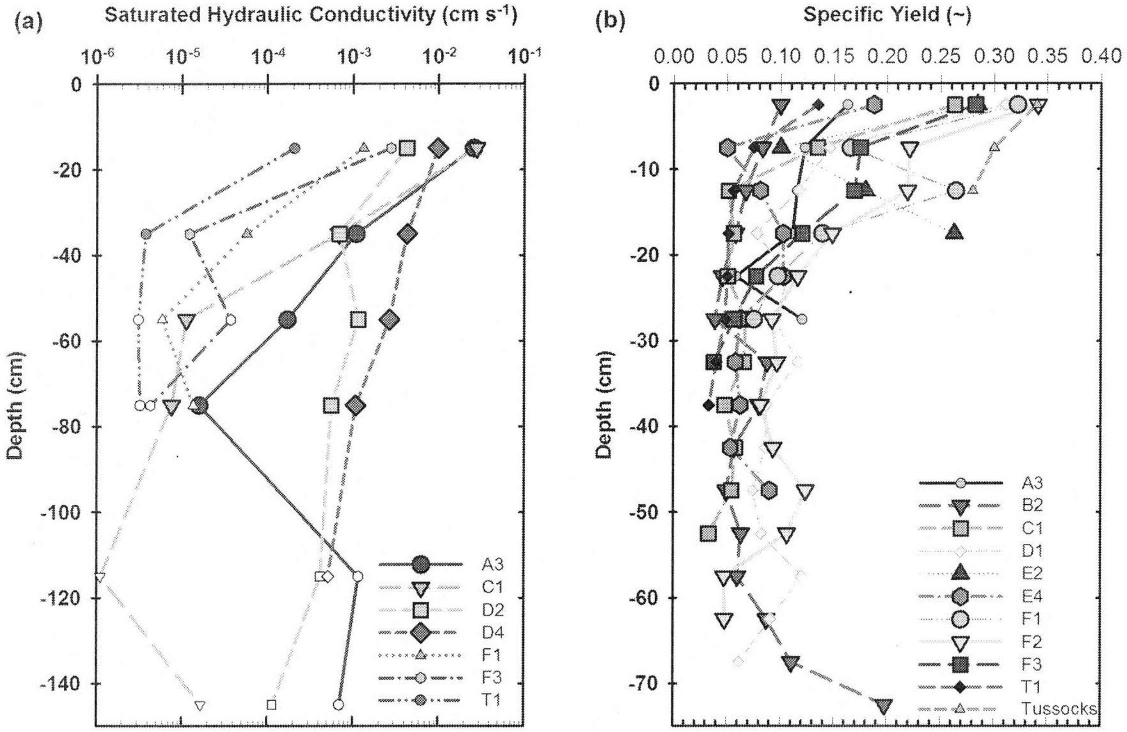


Figure 3.2: Peat and soil physical properties; (a) saturated hydraulic conductivity, and (b) specific yield. Labels refer to piezometer nest locations from Figure 1. The open symbols in (a) indicate measurements from the mineral soil underlying calcareous fen peat.

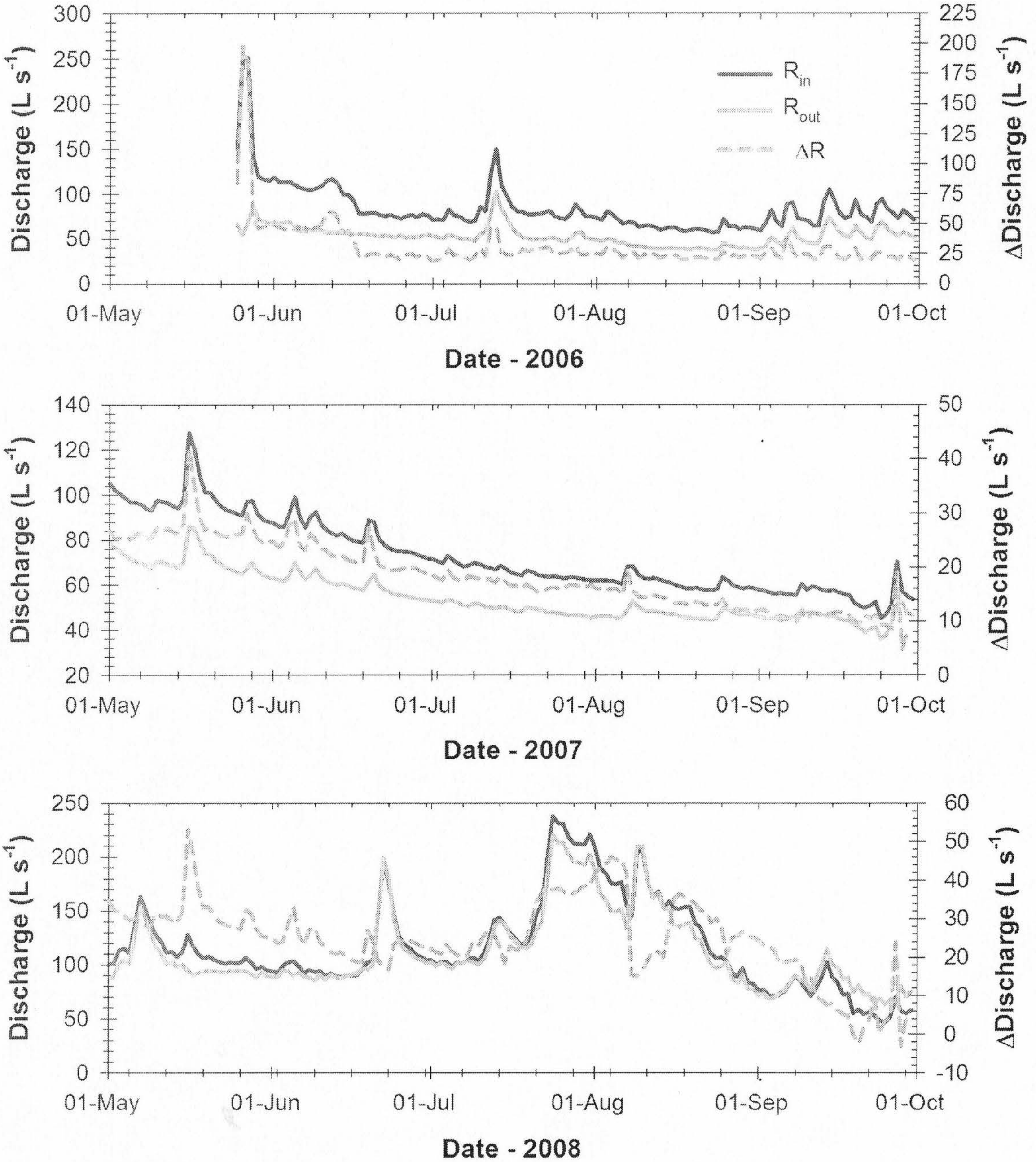


Figure 3.3: Fletcher Creek discharge at the entrance and exit to the Riparian Fen in each of the three study growing seasons, with daily average difference between gauging stations. (Note: positive difference values indicate water retention in the Riparian Fen).

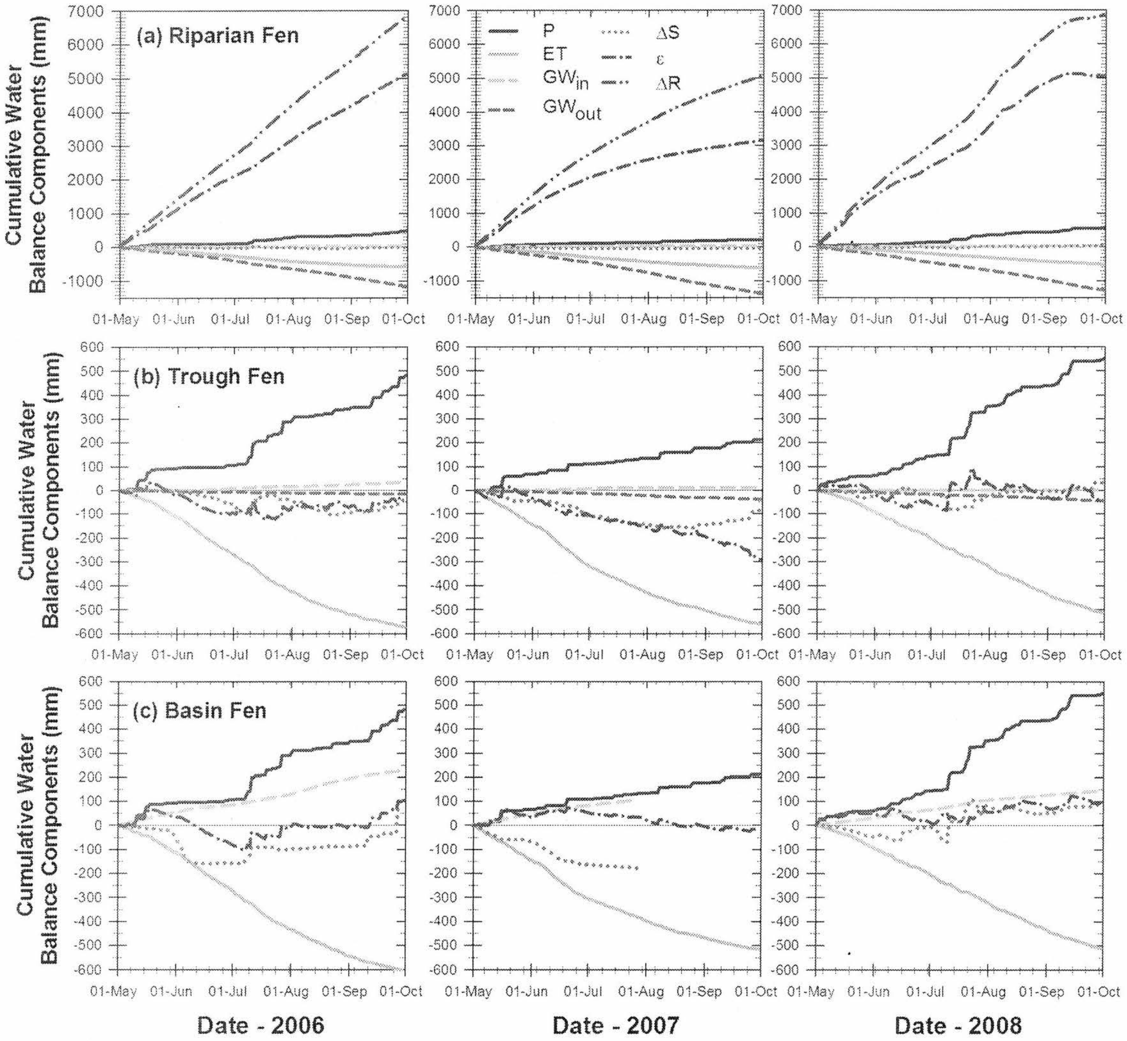
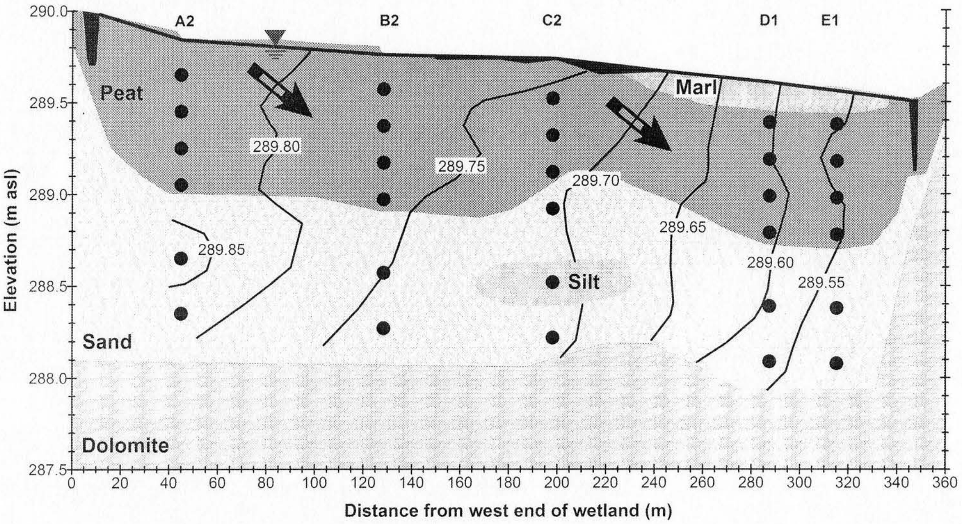


Figure 3.4: Water balances for the normal-2006, dry-2007, and wet-2008 growing seasons for the (a) Riparian Fen, (b) Trough Fen, and (c) Basin Fen. Legend symbols correspond to components of Equation 1.

(a) Wet Period Cross-Section Along West-East Axis



(b) Dry Period Cross-Section Along West-East Axis

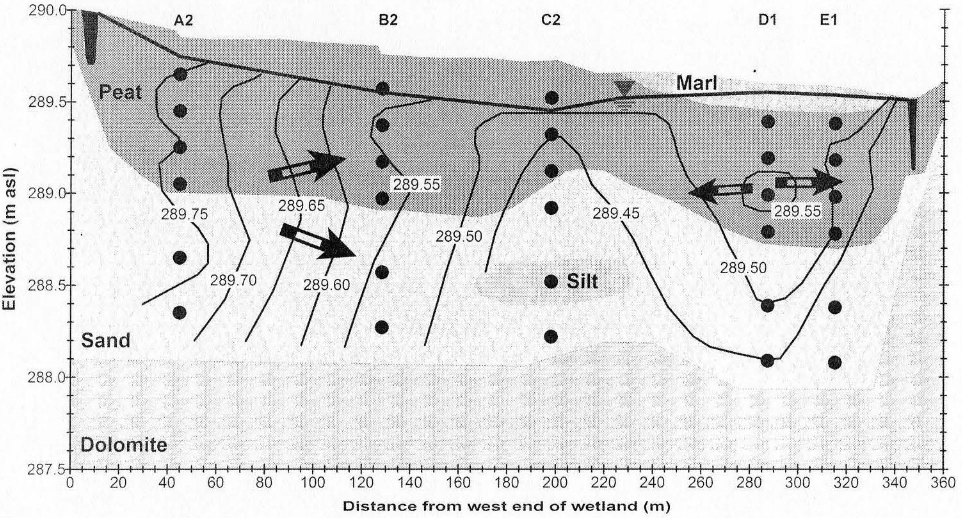
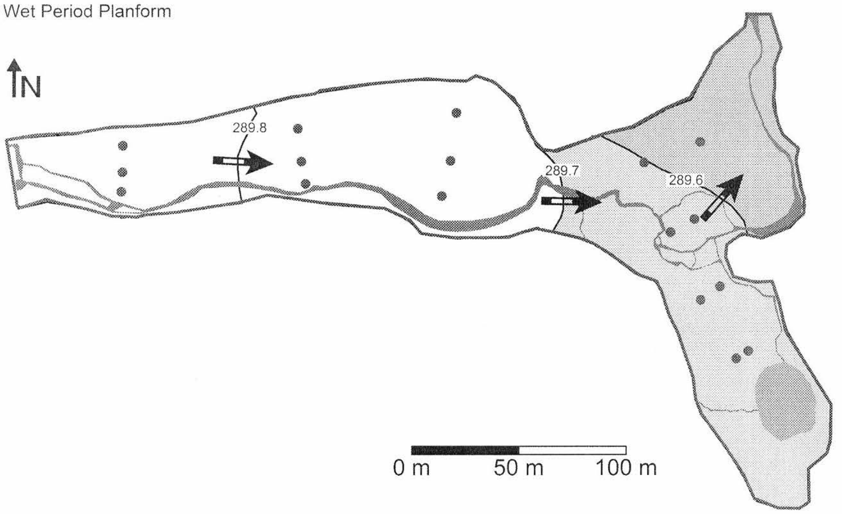
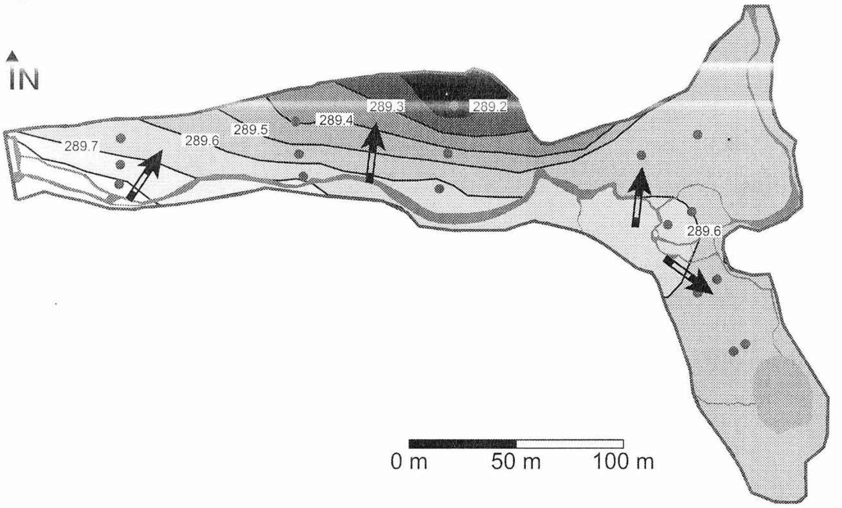


Figure 3.5 a-b: Hydrodynamics of the Riparian Fen in cross-section (a-b) and planform (c-d) representative of wet (a & c) and dry (b & d) conditions. Cross-sections depict hydraulic gradients between piezometers with equipotential lines at a 5-cm interval, with associated stratigraphy. Vertical exaggeration is 75X. Planform images depict water table elevation; colour shading is black-to-white across the range on water table positions observed for the Riparian Fen; contour interval is 10 cm.



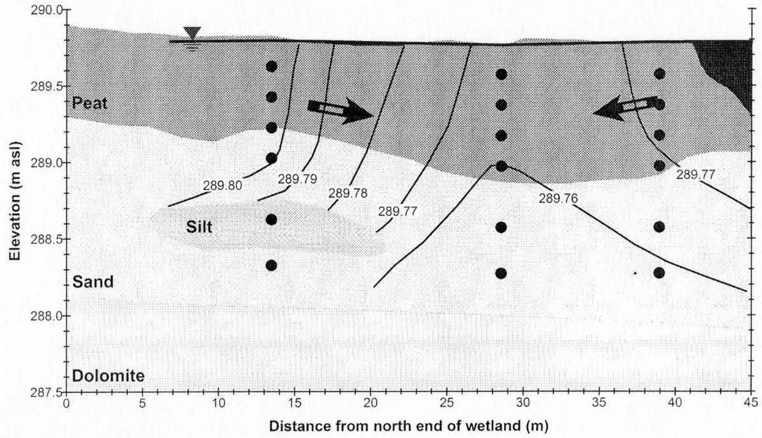
(c) Wet Period Planform



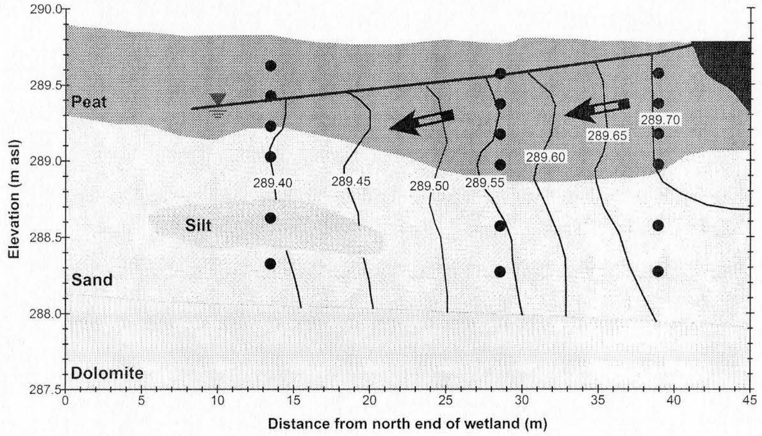
(d) Dry Period Planform

Figure 3.5 c-d: Hydrodynamics of the Riparian Fen in cross-section (a-b) and planform (c-d) representative of wet (a & c) and dry (b & d) conditions. Cross-sections depict hydraulic gradients between piezometers with equipotential lines at a 5-cm interval, with associated stratigraphy. Vertical exaggeration is 75X. Planform images depict water table elevation; colour shading is black-to-white across the range on water table positions observed for the Riparian Fen; contour interval is 10 cm.

(a) Wet Period Cross-Section of B-Transect



(b) Dry Period Cross-Section of B-Transect



(c) Cross-Section of D-Transect Representative of All Conditions

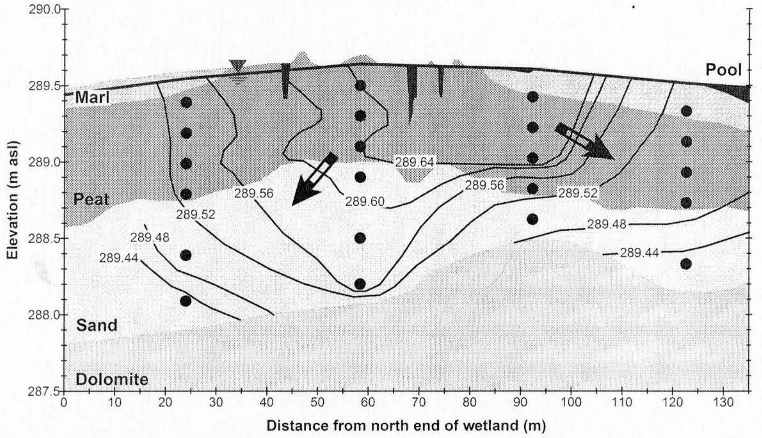
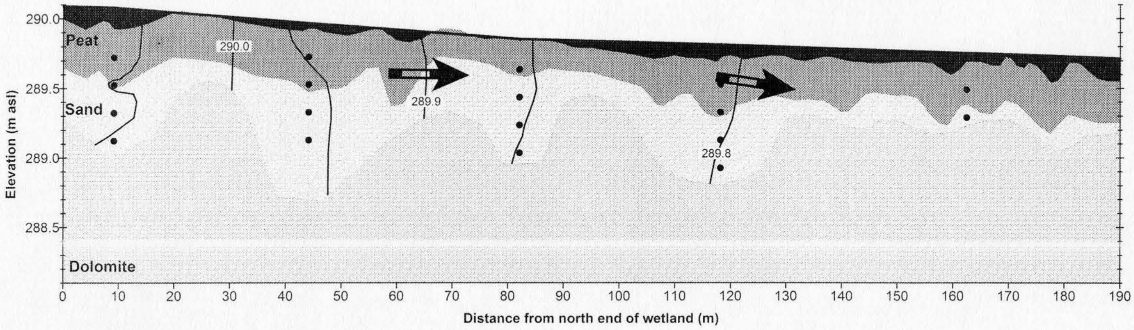
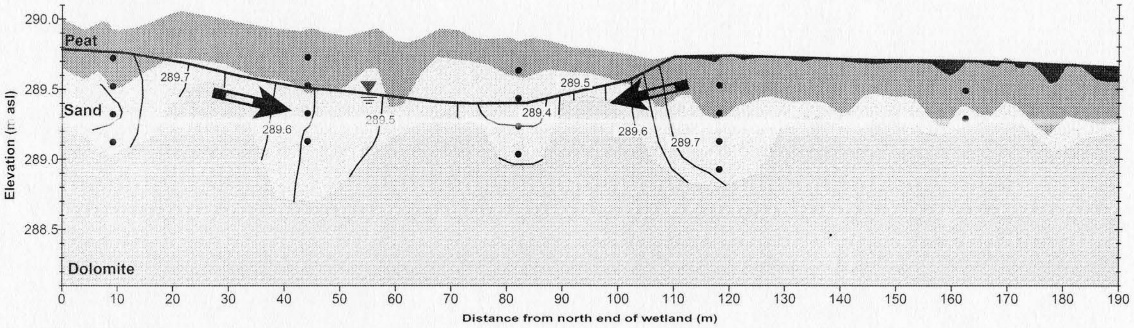


Figure 3.6: Representative cross-sections of hydraulic gradients along the B-transect under (a) wet and (b) dry conditions and the (c) D-transect of the Riparian Fen. Vertical exaggeration is 10X. Equipotential line interval is 1, 5, and 4 cm in (a), (b), and (c), respectively.

(a) Wet Period Cross-Section



(b) Dry Period Cross-Section



(c) Wet Period Planform (d) Dry Period Planform

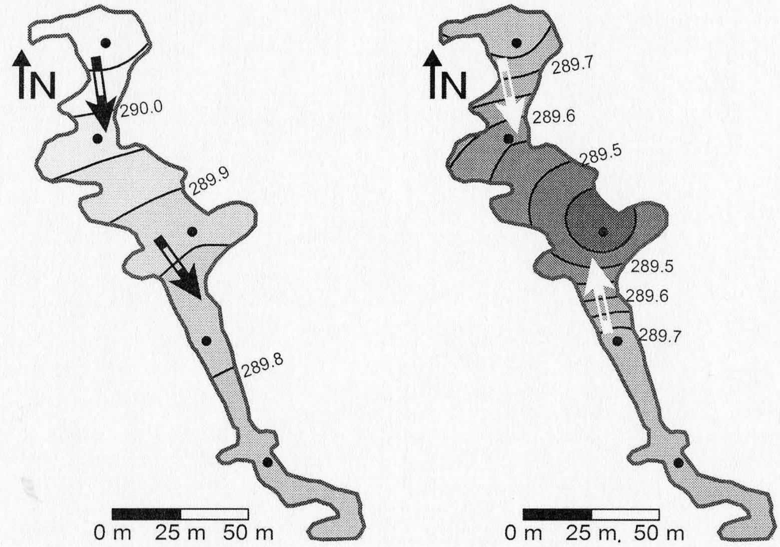
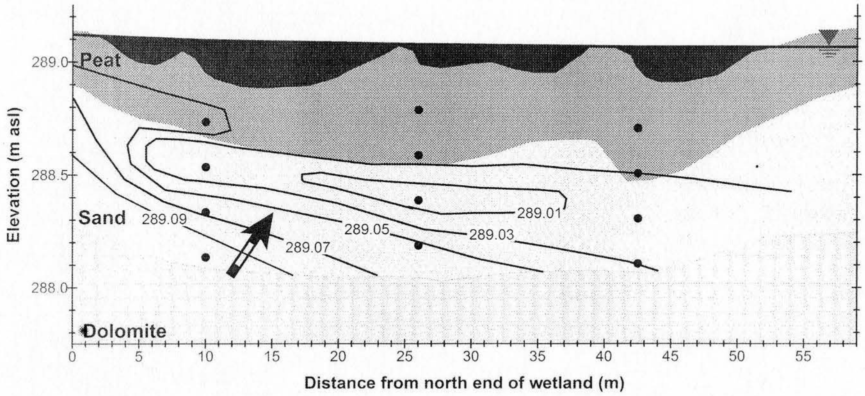
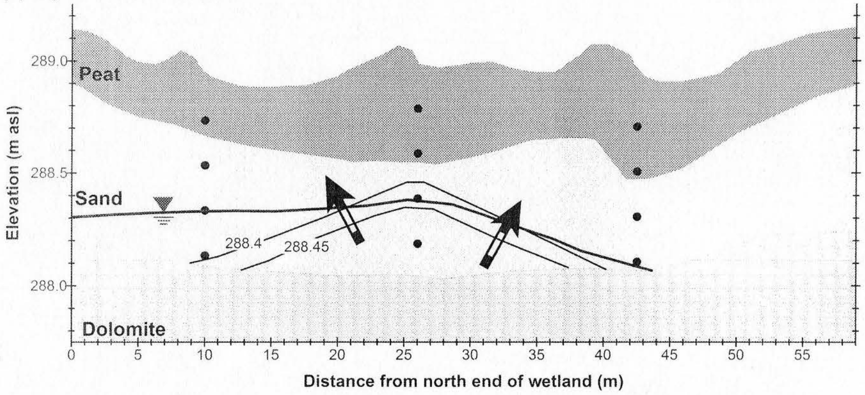


Figure 3.7: Hydrodynamics of the Trough Fen in cross-section (a-b) and planform (c-d) representative of wet (a & c) and dry (b & d) conditions. Cross-sections depict hydraulic gradients between piezometers with equipotential lines at a 5-cm interval. Vertical exaggeration is 25X. Planform images depict water table elevation; colour shading is black-to-white across the range on water table positions observed for the Trough Fen; contour interval is 5 cm.

(a) Wet Period Cross-Section



(b) Dry Period Cross-Section



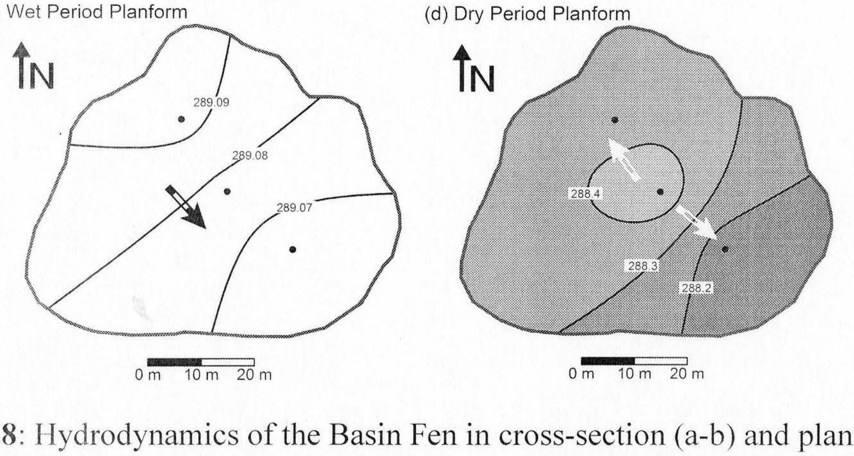

(c) Wet Period Planform (d) Dry Period Planform

Figure 3.8: Hydrodynamics of the Basin Fen in cross-section (a-b) and planform (c-d) representative of wet (a & c) and dry (b & d) conditions. Cross-sections depict hydraulic gradients between piezometers; equipotential line interval is 2 cm in (a) and 1 cm in (b). Vertical exaggeration is 17X. Planform images depict water table elevation; colour shading is black-to-white across the range on water table positions observed for the Basin Fen; contour interval is 1 cm in (c) and 10 cm in (d).

CHAPTER 4:
REDOX BUFFERING AND CALCITE PRECIPITATION IN CALCAREOUS FENS: CONSTRAINTS ON PHOSPHORUS AVAILABILITY

4.1 Abstract

Nutrient limitation is a strong control on the high species richness and diversity of calcareous fens, and can be influenced by coupled biogeochemical cycles, particularly redox reactions and calcium carbonate equilibria. We studied spatial patterns in relevant pore-water chemistry throughout a growing season to investigate controls on nutrient, particularly phosphorus, bioavailability in three hydrogeomorphologically distinct calcareous fens in southern Ontario, Canada: a Riparian Fen, a Trough Fen, and a Basin Fen. Phosphate-P and nitrate-N were very low (mean ±1SD = 11 ±4 μg L^{-1} and 17 ±52 μg L^{-1}, respectively), while ammonium-N and potassium were much higher (307 ±643 μg L^{-1}, 1.52 ±0.97 mg L-1, respectively), and there was significant variability among sites, month, and depth of peat and mineral layer. Spatial patterns of nutrient availability demonstrated a dependence on redox gradients that were in line with the dominant hydrological flowpaths. Unlike other calcareous fens very low iron levels precluded significant control by iron chemistry on P-availability. Between 15 and 40 % of the total dissolved phosphate was unavailable to vegetation due to high calcium and magnesium carbonate levels, which was explained by the saturation index of calcite (R^2 = 0.90). These results demonstrate that tremendous P-limitation can occur in calcareous fen pore-water in low-Fe sites, and that hydrogeomorphic-induced water flow paths control known redox buffers and gradients in calcareous fens. Determination of the range of controls on P-availability is necessary for process-based determination of within-site vegetation distribution in calcareous fens and implementation of sound management practices.

4.2 Introduction

Calcareous fens are wetlands fed principally by water rich in calcium, magnesium, and bicarbonate (Almendinger and Leete, 1998b; Komor, 1994), have accumulated more than 40 cm of peat (Mitsch and Gosselink, 2007; National Wetlands Working Group, 1997), and have near-surface soil and surface water pH in the range of 6.0 to 7.8 (Bedford and Godwin, 2003; Eggers and Reed, 1987). Dominated by sedges and brown mosses, calcareous fens exhibit very high vascular and non-vascular vegetation species richness and diversity (Johnson and Steingraeber, 2003; Motzkin, 1994), serve as regional refugia for a number of rare plant taxa (Bowles et al., 2005; Nekola, 1994) and are a focus of conservation and restoration efforts for these biodiversity values (Cooper and MacDonald, 2000; Lamers et al., 2002; Middleton et al., 2006). The high species richness and diversity appear to be related to the scarcity of inorganic phosphorus in the fen peat and pore-water (Boyer and Wheeler, 1989; Lucassen et al., 2004b; Nekola, 2004; Wassen et al., 1990). This study aims to determine the biogeochemistry and bioavailability of nutrients, particularly phosphate, in calcareous fen pore-water.

The vast majority of the phosphorus in a fen ecosystem resides in the peat and mineral sediment. Between 30 and 85 % of the total P of a fen is organic-P bound to the peat material (Pérez Corona et al., 1996). The inorganic-P is a combination of calcium carbonate-incorporated phosphate ($CaCO_3$~PO_4, calcium phosphate (apatite, $Ca_3(PO_4)_2$), iron-(oxy)hydroxide-bound phosphate ($Fe(OOH)$-PO_4), aluminum phosphate ($AlPO_4$), as well as amorphous Al- and Fe-PO4 complexes (Banach et al., 2009; Shenker et al., 2005; Zak et al., 2004). Recently, it has been shown that phosphate biogeochemistry in these extreme rich fens is tightly coupled to a number of other biogeochemical cycles, particularly iron, even with the elevated calcium levels (Boomer and Bedford, 2008b; Zak and Gelbrect, 2007). Golterman (1988) demonstrated that once in sediment, most of the PO_4^{3-} is bound to iron hydroxides, even if it came out of solution associated with calcium carbonate. Redox reactions are important controls on phosphate availability as Fe^{3+} reduction leads to the mobilization of this iron-bound P, particularly when combined with sulphate (SO_4^{2-}) reduction, as the resultant FeS_x compound allows the liberated PO_4^{3-} to move into solution (Lucassen et al., 2004a). High nitrate (NO_3^-) concentrations and denitrification serve as a redox buffer on Fe^{3+} and SO_4^{2-} reduction, limiting P-release through this process (Hedin et al., 1998; Lucassen et al., 2004b). High chloride (Cl^-) and SO_4^{2-} concentrations can also lead to PO_4^{3-} mobilization, through anion exchange on available binding sites (Beltman et al., 2000). Most of the above knowledge has been determined in controlled laboratory incubations and mesocosm studies seeking to effect a change in peat and soil biogeochemistry to elicit a response in fen pore-water. The spatiotemporal distribution of available PO_4^{3-} in relation to other pore-water constituents in the natural field setting has received less attention.

Previous research on calcareous and rich fen nutrient dynamics has sampled the pore- and surface water once or twice, most commonly early in the growing season and after plant senescence (Almendinger and Leete, 1998a; Bowles et al., 2005; Komor, 1994; Lucassen et al., 2006; Wassen and Joosten, 1996). Furthermore, many studies have sought to characterize between-fen differences in nutrient status and vegetation patterns, investigating numerous calcareous fens within a region, but only sampling in one to a few sampling points per fen (Amon et al., 2002; Johnson and Steingraeber, 2002; Motzkin, 1994; Nekola, 2004; Vitt and Chee, 1990). This is somewhat surprising, as calcareous fens are known to have distinct spatial patterning of vegetation within a site (Boyer and Wheeler, 1989). Additionally, hydrogeologic (Godwin et al., 2002; McNamara et al., 1992) and hydrogeomorphic (Chapter 3) setting have been found to significantly affect surface and subsurface calcareous fen hydrology, and these flowpaths have been shown to control redox gradients and influence peat soil nutrient chemistry (Boomer and Bedford, 2008a: 2008b). Evidence exists that within-site species distribution is related to calcareous fen hydrology and soil chemistry (Boeye and Verheyen, 1994; Hájková et al., 2004), but there is currently a disconnect between correlation studies and process-based studies on the distribution of available plant nutrients.

In this study we examine the spatial and temporal variability of pore-water nutrient dynamics in calcareous fens of contrasting landscape position (hydrogeomorphic setting). Specifically, our objectives were to answer the following questions: (1) What is the nutrient status of calcareous fen pore-water throughout a growing season? (2) How does hydrogeomorphic setting affect the growing season nutrient availability? (3) Is there evidence of coupling of biogeochemical cycles at the ecosystem-scale, and does this coupling affect nutrient status? And (4) what are the controls on the bioavailability of phosphate in calcareous fen pore-waters. Determination of the variation in P-availability and its controls is a necessary step in process-based elucidation of within-site vegetation zonation of calcareous fens, and will aid sound management and restoration decisions of these biodiverse but potentially sensitive ecosystems.

4.3 Study Area

The three calcareous fens are located in a 332 ha headwater catchment of the Spencer Creek Watershed, 70 km west of Toronto, Ontario, Canada (43° 24' 57" N, 80° 7' 3" W). Greater detail of the catchment underlain by dolomite and the study fens can be found in Chapter 2. For ease of comparison the unnamed fens are designated by their hydrogeomorphic position, using the nomenclature of Brinson (1993) and Godwin et al. (2002). At 4.5 ha the largest calcareous fen in the catchment is the Riparian Fen, traversed by the second order Fletcher Creek. It is gently sloping, with only 30 cm elevation change across 450 m of stream length (stream gradient of 0.00067). Vegetation of this site is variable, with the western half a mixture of fen sedges (*Carex flava* L., *C. livida* (Wahlenb.) Willd., *Rhynchospora alba* (L.) Vahl) and shrubs (*Rhamnus alnifolia* L'Hér., *Cornus stolonifera* Michx., *Rubus pubescens* Raf). The eastern half is primarily sedge-dominated (*Carex aquatilis* Wahlenb., *C. prairea* Dewey ex Alph. Wood, *C. livida* (Wahlenb.) Willd.) with areas of *Menyanthes trifoliata* L., *Scirpus acutus* Muhl., and *Lysimachia thyrsiflora* L. co-dominance. A small pool occupies the southern-most portion, which is surrounded by calcite precipitate known as a marl flat (Miner and Ketterling, 2005).

The intermediate-sized fen (2 ha) is a Trough Fen. The minimum distance from the edge of the Trough Fen to Fletcher Creek is 20 m at points at the northernmost, middle, and southernmost portions of the fen. Elsewhere, the fen is separated from the stream by 40-75 m of riparian swamp. Vegetation in the Trough Fen is generally sedge-dominated (*Carex lacustris* Willd., *C. stricta* Lam., *C. lasiocarpa* Ehrh.) with co-dominance of grasses (*Calamagrostis canadensis* (Michx.) P. Beauv.) to the north, herbaceous species (*Eupatorium maculatum* L., *Lycopus uniflorus* Michx.) in the middle-north, rushes (*Juncus canadensis* J. Gay ex Laharpe) in the middle-south, and cattails (*Typha angustifolia* L.) in the south. There is 43 cm of elevation change along the 200 m length of the wetland.

The smallest wetland studied was the Basin Fen. It is only 0.45 ha is size, and occupies a gentle depression in the upland cedar forest. There is at least 100 m of cedar upland or cedar swamp between the Basin Fen and Fletcher Creek, with no surface connection. The vegetation of the Basin Fen is sedge-dominated (*Carex stricta* Lam., *Carex utriculata* Boott, *Dulichium arundinaceum* (L.) Britton) with co-dominance of willow shrubs (*Salix pedicellaris* Pursh, *S. petiolaris* Sm.). Elevation of the fen floor varied by only 15 cm; however, the formation of tussocks of peat up to 70 cm above this fen floor by Upright Sedge (*C. stricta*) led to a highly variable surface topography.

4.4 Methods

4.4.1 Water Chemistry

In each of the fens a network of piezometers were installed in the peat and underlying mineral substrate for hydrologic measurements and water sampling (Figure 4.1; Chapter 2). Each nest of piezometers consisted of four to six piezometers at nominal depths of 20, 40, 60, 80, 120, and 150 cm (depth reflects bottom of the slot zone). At some nest locations bedrock was reached before placement of the 120 and/or 150 cm piezometers was possible. Water level measurements are described in detail elsewhere (Chapter 2).

Water samples were collected monthly during the 2008 growing season (May – August) in all piezometers containing water and not inundated, in addition to representative standing water and stream samples. Prior to collection, piezometers were purged of at least one standing volume of water using a hand pump connected to a volumetric flask and 0.5-cm diameter Tygon® tubing and allowed to re-fill (in some cases this required ~ 24hrs). Water from the piezometers was sampled with 0.25-cm diameter Tygon® tubing connected to a 60-mL plastic syringe with a three-way stopcock to prevent contact with the ambient air. Samples were transferred to 50-mL polypropylene tubes and placed on ice for transport to lab. Upon return to the lab, samples were immediately filtered through 0.7 μm glass-fiber-filter papers using a vacuum apparatus. One set of samples were subsequently acidified to $pH < 2$ with concentrated nitric acid and stored at 3°C until analysis for major cations and another set of samples were frozen at -25°C unacidified until analysis for nutrients, chloride, and sulphate.

During the May sampling date separate water samples were obtained for field determination of pH, electrical conductivity (EC), dissolved oxygen (DO) content, and temperature (T), as well as alkalinity determination. Calibration of the pH and EC meters were made in the field just prior to use; DO was analyzed using a luminescent dissolved oxygen sensor with a manufactured calibration. Accuracy for pH, EC, T, and DO was ±0.01 units, $\pm 20\ \mu S\ cm^{-1}$ with automatic temperature compensation, ±0.5°C, and $\pm 0.1\ mg\ L^{-1}$, respectively. Samples for alkalinity determination were stored without headspace by overfilling sample tubes, tightly sealed, and stored on ice for transport to the lab. Analysis was made using a HACH® digital titrator with 1.6N H_2SO_4 titrant within 24 hrs of sample collection. Initial lab-measured pH during alkalinity titration was always within 0.05 units of field determination. Alkalinity titration accuracy was ±0.5 %, or $\pm 30\ \mu eq\ L^{-1}$ over the range of sample alkalinity.

A standard 10 % QA/QC protocol was followed for all analytes, except for phosphate, where QA/QC was 20 %. Measurements of chloride, ammonium, nitrate, and phosphate were made on a Technicon® auto-analyser colorimeter using the ferricyanide, Berthelot, sulphanilamide following cadmium reduction, and the molybdate blue methods, respectively (Environment Canada, 1979). Minimum detection limits (MDL) for Cl^-, NH_4^+-N, NO_3^--N, and PO_4^{3-}-P were $0.1\ mg\ L^{-1}$ and 8, 4, and $2.5\ \mu g\ L^{-1}$, respectively. Accuracy for Cl^-, NH_4^+-N, NO_3^--N, and PO_4^{3-}-P was determined to be ±0.5 %, 1 %, 2 %, and 5 %, respectively, in the range of sample concentration. Analysis of phosphate was run for both acidified and unacidified sample sets. Dissolved organic carbon was determined using a Lachat® IL550 TOC-TN analyzer, with accuracy and MDL of 0.1 and 0.75 mg L^{-1}. Analysis of major cations was done on a Perkin Elmer® Aanalyst 400 atomic absorption spectrometer. Analytical accuracy for cations was 0.02 ppm and minimum detection limit was 0.01 ppm. Because of unknown matrix effects, lanthanum oxide was added to the samples to a final concentration of 1 % to enhance absorption and detection of calcium and magnesium. Determination of sulphate on unacidified samples was done on a Dionex® 3100 ion chromatograph with suppression and conductivity detection.

4.4.2 Data Analysis

Initial observation and hydrologic interpretation suggested that the western and eastern halves of the Riparian Fen were hydrologically and biogeochemically different; therefore, the two areas were treated separately, with piezometer transects A, B, and C comprising the Riparian West site, and transects D and E and additional nests representative of the East site. A three-way fixed effects ANOVA was conducted to assess the effects of site, depth, and sampling month on measured and calculated nutrient variables. To allow for this statistical comparison only the B and D transect piezometers were included to represent the Riparian West and East sites, respectively. Additionally, data were grouped into three depth categories (upper peat, lower peat, and mineral substrate) to accommodate the different depths between sites. Nutrient data were log-transformed to improve homoscedasticity and normality of residuals. Post-hoc Tukey's HSD tests were run to determine statistical significance among means. Pearson correlation coefficients were calculated to assess relationships among pore-water chemical constituents. All statistical tests were performed using SYSTAT 12 (SYSTAT, 1997). To graphically illustrate spatial trends in redox-sensitive elements the Kriging method of interpolation was used in Surfer 7 (Golden Software, 1999). Resultant cross-sections represent seasonal average trends. The geochemical package PHREEQC (Parkhurst and Apello, 1997) was used to calculate speciation of measured analytes and saturation indices of relevant minerals from the May set of pore-water samples.

4.5 Results

4.5.1 Calcareous Fen Hydrology

The dynamics of water table fluctuation and subsurface flow paths in the calcareous fens have been presented elsewhere (Chapter 2; Chapter 3). The general directions in water movement within the fens are identified in Figure 4.1. Briefly, the 2008 growing season was especially wet, with saturation of the peat profile for nearly the entire growing season across much of the fens (Chapter 2). Fletcher Creek served as the principal source area of water to the Riparian Fen, both through sustained streambank seepage and overbank flooding during rain events (Chapter 3). The Trough Fen was dominated by precipitation inputs and an ephemeral rivulet and subsurface connection to Fletcher Creek and the adjacent riparian cedar swamp. The Basin Fen received significant groundwater discharge as well as precipitation inputs during the study period.

Subsurface hydraulic gradients in the Riparian Fen were quite low, with flow paths in the West section directed both inland from the stream and from the northern fen edge following the general topography, allowing for approximately 5 cm of lateral subsurface movement over the growing season. In the East portion, stream recharge into the peat dominated subsurface flow paths. Subsurface water movement followed the topography of the Trough Fen, with gentle hydraulic gradients of 0.002, minimizing lateral movement: there were also limited vertical hydraulic gradients within the nests. The subsurface hydrology of the Basin Fen was dominated by groundwater upwelling, with vertical hydraulic gradients being an order of magnitude larger than horizontal gradients (0.075 vs. 0.002).

4.5.2 Nutrient Variability in Calcareous Fen Pore-water

The four sites differed in pore-water phosphate ($P < 0.01$), ammonium ($P < 0.001$), and potassium ($P < 0.001$) concentrations, but not nitrate ($P > 0.05$; Table 4.1). This resulted in significant differences in N:P and N:K ratios, and the percentage of inorganic nitrogen present as ammonium between sites ($P < 0.001$; Table 4.1). Ammonium ($P < 0.01$) and potassium ($P < 0.001$) levels differed with depth, while phosphate ($P < 0.01$) and nitrate ($P < 0.001$) levels differed most significantly with growing season month. There were also significant interaction effects of site and depth on nitrate ($P < 0.01$), ammonium ($P < 0.05$), potassium ($P < 0.001$), and N:P ratio ($P < 0.05$), as well as site and month on phosphate ($P < 0.01$) and nitrate ($P < 0.05$; Table 4.1).

The effect of site on phosphate concentrations determined from the acidified samples was more significant than on the unacidified samples (F-ratio of 12.08 vs. 4.01 and $P < 0.001$ vs. $P < 0.01$; Table 4.1). This also led to a significant difference in the ratio of phosphate determined on acidified samples compared to unacidified samples between sites ($P < 0.001$). Inclusion of all data demonstrates a wide range of phosphate determination from the same piezometer samples (Figure 4.2). Across all sites, there were many piezometers where acidification did not increase measured phosphate levels (falling on the 1:1 line of Figure 4.2). Most of the samples obtained yielded between 1 and 5X more phosphate when acidified prior to determination; however, there were several samples, mainly from the Riparian West site, with greater than 5X more phosphate detected upon acidification. This ratio did not vary systemically with increasing concentration, pH, sample month, depth, or distance to source waters. Unless stated otherwise, the following presentation of the results is based on the unacidified sample determination.

The Riparian East site had the highest pore-water phosphate-P levels, and at 12.4 $\mu g\ L^{-1}$ was significantly greater than the Trough Fen, which was lowest at 9.5 $\mu g\ L^{-1}$ (Table 4.2). Ammonium-N concentrations were also greatest in the pore-water of the Riparian East Fen, averaging 808.1 $\mu g\ L^{-1}$, which was more than an order of magnitude greater than the Trough Fen mean of 56 $\mu g\ L^{-1}$. The high pore-water ammonium concentration in the Riparian East site led to a very high N:P molar ratio of 134, which was nearly 10X greater than the Trough Fen (Table 4.2). The low ammonium levels in the Trough Fen resulted in just 77 % of the inorganic nitrogen being in the NH_4^+ form, which was significantly lower than the other sites, which were all greater than 90 %. Nitrate-N levels did not vary significantly across sites or with depth, but did increase as the growing season progressed, from a mean of 10 $\mu g\ L^{-1}$ in May to 30 $\mu g\ L^{-1}$ by the end of August (Table 4.2). Ammonium concentrations were > 3.5X higher in the peat samples than the underlying mineral, while the lower peat and mineral layers contained higher potassium levels than the upper peat. The N:P ratio of 70 – 76 in June and July was twice as large as the May sampling date (Table 4.2). N:K ratios averaged less than 1 in each sampling month, but increased as the growing season progressed.

The variability in phosphate within each site fluctuated between months, with the Riparian West, Riparian East, Trough, and Basin Fens having their largest ranges in July, May, June, and August, respectively (Figure 4.3a), though the May samples from the Riparian East site clearly appeared to be higher than the remaining sites and months. There were no obvious trends in the variability in nitrate-N across the sites and growing season (Figure 4.3b). A large number of nitrate-N levels below detectable limits led to the median values being much closer to the 25% percentile than the 75% percentile in most instances. There were many more high nitrate-N concentration outliers in the Riparian Fen than the Trough or Basin Fens. While median values of ammonium-N were all around 50 to 175 μg L^{-1} across the studied fens, the ranges were clearly higher in the Riparian Fen, especially in the East portion of the fen, with a very homogenous distribution in the Trough Fen (Figure 4.3c). The Riparian East Fen also had persistent outliers of > 3 mg L^{-1}, which was more than an order of magnitude greater than the median values. Median potassium concentration in the Riparian West Fen of ~ 2 mg L^{-1} was twice as high as the other sites, and the potassium ranges decreased from Riparian West, to the East and the Trough Fen and was lowest in the Basin Fen (Figure 4.3d).

Because of the large sample size several bivariate relationships among pore-water constituents were assessed as significant, even though the correlation coefficients were quite low (e.g., phosphate-P was significantly correlated with Cl- at the $P < 0.001$ level, but with only 0.15 correlation coefficient; Table 4.3). However, there were several correlations that warrant attention. Most notably, phosphate-P was significantly correlated with ammonium-N (Pearson's $r = 0.52$, $P < 0.001$). The negative correlation of nitrate-N with % N as ammonium ($r = -0.64$, $P < 0.001$) suggests it is principally nitrate levels that determine the speciation of inorganic nitrogen, and not ammonium levels. In contrast, the very higher correlation of ammonium-N with the N:P and N:K ratios ($r = 0.91, 0.84$, respectively, $P < 0.001$) clearly demonstrate the importance of this form of nitrogen in the nutrient status of the fen pore-waters (Table 4.3). The calcium and magnesium concentrations exhibit a significant control on the electrical conductivity of the pore-water ($r = 0.70$, $P < 0.001$), and higher magnesium levels correlated with decreased pH ($r = -0.55$, $P < 0.001$). The pH of the fen pore-water was negatively related to the DOC concentration ($r = -0.64$, $P < 0.001$), demonstrating that the organic acids impart appreciably to these systems (Table 4.3). While not significant as per the linear Pearson Correlation test, there was a characteristic L-shape relationship between nitrate and ammonium (data not shown). All water samples contained iron and aluminum concentrations below MDL's of 0.01 mg L^{-1} (data not shown).

4.5.3 Spatial Variability in Redox-sensitive Ions

The spatial variability in phosphate and inorganic nitrogen were related to the hydrologic flow paths within the studied calcareous fens (Figures 4.4-4.7). Bioavailable phosphate levels in Fletcher Creek that recharged into the peat in the Riparian Fen averaged 8.6 μg L^{-1} during the 2008 growing season, whereas total dissolved phosphate (acidified samples) was 50 % greater at 12.1 μg L^{-1}. Phosphate levels increased slightly in the Riparian West Fen along the inland subsurface flowpath to greater than 12 μg L^{-1} 15 m from the stream (Figure 4.4a). Elevated stream water nitrate-N levels averaging 2.27 mg L^{-1} were quickly removed as the water migrated inland from the stream, with concentrations below 0.3 mg L^{-1} in piezometers just 3 m from the stream (Figure 4.4b). Nitrate-N levels continued to decline along the hydrologic flowpaths in the Riparian West Fen, reaching < 6 μg L^{-1} in the lower peat 15 m inland, as well as much of the underlying sands (Figure 4.4b). Stream and surface water ammonium-N concentrations averaged 42 μg L^{-1}, and pore-water NH_4^+-N levels increased along the hydrologic flowpaths to > 400 μg L^{-1} in the middle row of Riparian West piezometers (Figure 4.4c). Pore-water sulphate concentrations were greatest in the peat adjacent to the stream channel in the Riparian West site and progressively decreased with increasing distance from the stream, from > 100 mg L^{-1} to < 10 mg L^{-1} (Figure 4.4d). The zone of maximum phosphate concentrations in the Riparian West Fen was coincident with minimal nitrate and maximal ammonium levels.

With three distributaries and a backwater pool, the connection to Fletcher Creek was even more prominent in controlling nutrient levels in the Riparian East site (Figure 4.5). The low phosphate-P levels of Fletcher Creek increased to > 20 μg L^{-1} in the peat and sand surrounding the stagnant pond (Figure 4.5a). Inorganic nitrogen patterns were similar to the Riparian West site as nitrate-N concentrations decreased along the stream recharge flowpaths (Figure 4.5b), and ammonium-N levels greatly increased in the southern-most areas of the Riparian East site, to over 3 mg L-1 in the surface peat (Figure 4.5c). Sulphate concentrations were much lower in the Riparian East site relative to the West site, but generally followed the same trend of declining concentrations with increasing distance from surface waters (Figure 4.5d). Maximum phosphate-P and ammonium-N and minimum nitrate-N pore-water concentrations were all centred around the D4 and E4 piezometers.

Despite the general downvalley hydraulic gradient along the Trough Fen, nutrient concentrations were more related to the underlying bedrock topography; that is, there were discreet sections of peat and sand with their own nutrient patterns separated by bedrock spurs (Figure 4.6). Phosphate-P concentrations were low (4 – 9 μg L^{-1}) in the F1, F3, and F5 nests and peaked in the upper peat of the F4 nest and the deeper sand of the F2 nest (12 – 15 μg L^{-1}; Figure 4.6a). Maximum nitrate-N levels were in the sand of the F4 nest and throughout the F3 nest, where concentrations ranged from 20 – > 100 μg L^{-1} (Figure 4.6b). Ammonium-N levels were significantly lower in the Trough Fen than elsewhere (Table 4.2), only reaching > 100 μg L^{-1} at greater than 70 cm depth in the F4 nest (Figure 4.6c). The northern half of the Trough Fen was distinctly lower (mean = 2.1 mg L^{-1}) than the southern half, where concentrations exceeded 100 mg L^{-1} (Figure 4.6d). Surface water samples in the Trough Fen contained on average 7.6 μg PO_4^{3-}-P L^{-1}, 46 μg NH_4^+-N L^{-1}, and 2.1 mg SO_4^{2-} L^{-1}, though the northern half surface water contained < 10 μg NO_3^--N L^{-1} throughout the season, whereas the southern half contained > 1200 μg L^{-1} in July and August.

Groundwater upwelling into the Basin Fen was low in phosphate-P (< 8 μg L^{-1}) with moderate nitrate-N (mean = 32 μg L^{-1}) and ammonium-N concentrations (mean = 122 μg L^{-1}), but very high sulphate levels (> 240 mg L^{-1}; Figure 4.7). As groundwater migrated outward and upward from the north end of the Basin Fen sulphate and nitrate levels decreased by 50 and 90 %, respectively, whereas phosphate and ammonium levels increased by 50 and 500 %, respectively (Figure 4.7). The southern portion of the fen displayed very little spatial variability, with uniformly low levels of all redox-sensitive pore-water constituents. Surface waters in the Basin Fen averaged 12 μg PO_4^{3-}-P L^{-1}, 53 μg NH_4^+-N L^{-1}, and 6.7 mg SO_4^{2-} L^{-1}, with nitrate-N concentrations below detectable limits.

4.5.4 Controls on the Availability of Phosphorus

Phosphate-P concentrations displayed a greater correlation with ammonium-N levels than with the percent of inorganic nitrogen present as ammonium (Table 4.3). This is primarily due to the non-linear relationship between phosphate and the percent N as ammonium in the May and June samples, and the non-responsive relationship in July and August (Figure 4.8). In the early growing season, most of the calcareous fen pore-waters contain > 70 % of inorganic nitrogen as NH4+, and high phosphate concentrations correspond to areas where > 90 % of the inorganic nitrogen is NH4+. In the latter portions of the growing season, fen pore-waters contained greater concentrations of nitrate-N without significant changes to ammonium content (Table 4.2), resulting in a wider distribution of the inorganic nitrogen ratio. Coincident with this shift in nitrogen speciation, phosphate-P concentrations were generally lower, without the high concentrations associated with the May and June sample dates (Figure 4.7).

Geochemical modelling of the May dataset using the phosphate determined from the acidified samples (liberating all phosphate) revealed the importance of the calcium carbonate system on phosphate availability (Figure 4.9). A very strong relationship (R^2 = 0.90) was calculated for the percentage of bio-available phosphate (as $H_2PO_4^-$ and HPO_4^{2-}) as a function of the saturation index of calcite in the fen pore-water. With iron and aluminum levels < 0.01 mg L^{-1}, the vast majority of the dissolved phosphate in the pore-water was present as $CaHPO_4$ and $MgHPO_4$ (data not shown). This relationship was ubiquitous across the sites, and indicates that samples ranged from > 85 % of phosphate freely available at moderately undersaturated conditions, to < 60 % under slightly supersaturated conditions, with 72 % of total dissolved phosphate bioavailable in solutions in equilibrium with calcite, regardless of total concentration (Figure 4.9).

Relationships with dolomite, aragonite, and hydroxyapatite were lower. There were no strong relationships of the free phosphate forms or the $SI_{calcite}$ with any other measured parameter, including calcium concentration, pH, temperature, or alkalinity, suggesting that there is not a simple metric for calculation of the bioavailable forms of phosphate. While the full suite of necessary parameters were only available for the May samples, presumably this relationship would remain the same throughout the growing season due to the balance of increased soil respiration raising pCO_2 (favouring calcite dissolution) and evapotranspirative water table drawdown (promoting CO_2 exsolution, increasing $SI_{calcite}$).

4.6 Discussion

Our results indicate that coupled biogeochemical cycles occur not only in fen peat studied in mesocosm fertilization and lab incubation studies (Beltman et al., 2000; Geurts et al., 2009; Kooijman and Hedenäs, 2009; Lucassen et al., 2004a; 2004b, 2006), but are dominant features across calcareous fen ecosystems. These coupled reactions are controlled in part by hydrological flowpaths as well as peat composition. Additionally, the seasonal progression of pore-water nutrient levels helps explain the high species diversity and spatial distribution of the vegetation in these calcareous fens. In the Riparian Fen elevated nitrate levels (> 2 mg NO_3^--N L^{-1}) in stream water recharge and overbank flooding were quickly removed along the hydrologic gradient inland: nitrate removal efficiencies of > 90 % were experienced within 3 m of the stream. This extreme concentration gradient was probably due to a combination of three processes: streamside plant uptake; denitrification; and the relatively low flux (0.3 L m^{-2} day^{-1}; Chapter 3) of water inland. Dissolved oxygen concentrations were always < 2.0 mg L-1 in the Riparian Fen pore-water, confirming anoxic conditions persisted through the fen. The lack of oxygen in the saturated fen pore-water prevented nitrification; hence, mineralization of organic nitrogen to ammonium led to an increase in ammonium levels along the dominant hydrologic flowpaths. Previous research has revealed sustained stream bank seepage leads to ammonium build-up in riparian sediments (Duval and Hill, 2007).

The delivery of elevated nitrate levels to the fen pore-waters provided a redox buffer on the bioavailability of phosphate. In June and July 2006 continuous measurements of redox potential indicated pore-waters at 20, 40, and 60 cm depth near the E2 nest were stable at +200 mV, whereas at the E1 nest redox potentials fluctuated between 0 and +100 mV (Duval, unpublished data). In contrast, redox potentials at the E4 nest ranged from –250 to –400 mV within the upper 60 cm of peat. Thus, the hydrologic process of stream recharge rich in oxygen and nitrate created a decreasing redox gradient with increasing distance from the source area, such that iron and sulphate reduction are only possible in well-defined areas of the Riparian Fen. A similar pattern developed in the Basin Fen, even with the much lower nitrate input (< 0.5 mg L^{-1}). This redox gradient corresponded with dissolved phosphate concentrations, which increased with increasing distance from source water areas in the Riparian and Basin Fens (Figures 4.4-4.6). This redox buffering on the bioavailability of phosphate is similar to the case of nitrate-rich groundwater in some Dutch fens (Lucassen et al., 2004a).

That concentrations of phosphate along this redox gradient were much lower than those found in similar studies is due to a number of factors. Firstly, while redox potentials were conducive to iron reduction 40 m from the stream channel, no iron was detected in the fen pore-water; that is, while we did not determine iron content in the peat and underlying sand, the lack of Fe^{2+} present in anoxic waters suggest the supply of iron-bound phosphate in the soil was small. This is in contrast to some New York rich fens, where iron-chemistry was the dominant control on phosphate cycling (Boomer and

Bedford, 2008b). Secondly, the very high calcium and magnesium concentrations ensured a sizable fraction of total dissolved phosphate was bound to these cations and not readily available to plants (Figure 4.9). Thirdly, the very high N:P ratios in the fen pore-water suggests a very high demand by the fen vegetation (Table 4.2). Such spatially extended redox gradients have been shown between fen types over 100s of metres (poor-rich fen gradients, Verhoeven et al., 1996), as well as through estuaries over kms (Jordan et al., 2008). In our sites this gradient over 10s of metres was presumably due to a lack of electron donors, as DOC was low in the Riparian Fen (~ 2 – 12 mg L^{-1}).

We did not determine dissolved sulphide concentrations in the pore-water; thus, the presence or absence of sulphate alone cannot be used as an indication of redox status. For instance, the low sulphate concentrations in the north half of the Trough Fen compared to the south half and Riparian and Basin Fens would suggest high levels of sulphate reduction in that area. However, there was no evidence of the accompanying ammonium build-up similar to the southern portions of the Riparian Fen. This, taken with hydrologic data that demonstrate the northern portion of the Trough Fen is rarely saturated for prolonged periods (Chapter 2), reveal that the low sulphate in that area is likely a sedimentological process, not a biogeochemical one. The Trough Fen appears to be formed from the peat build-up and coalescence of two basins that were once separated by a bedrock spur around the F3 nest; the northern half being derived of glacial outwash sands and gravels devoid of sulphate, the southern half developing on the dolomite bedrock with associated gypsum inclusions (Duval, unpublished data).

In contrast, hydrogen sulphide gas was very detectable by odour in the southern extent of the Riparian Fen, which was nearly always saturated (Chapter 2). Based on the > 1.5X interquartile range and > 90 % quantile concepts of Harms and Grimm (2008) and Mitchell et al. (2008), respectively, this area would be termed a persistent hotspot of both ammonification and sulphate reduction (*sensu* McClain et al., 2004) amongst the studied calcareous fens. It also had the highest pore-water phosphate concentrations, but the lowest species richness and standing biomass, presumably due to sulphide toxicity (Geurts et al., 2009). This was the only location of a marl flat in the fens, and was also a strong groundwater recharge zone (~67.5 L m^{-2} day^{-1}; Chapter 3). Marl flat formation in an area of sustained groundwater recharge does not conform to the conceptual model of marl flat formation in areas of groundwater discharge (Gilvear et al., 1992; Miner and Ketterling, 2006) or functioning of phosphate immobilization (Amon et al., 2002; Boyer and Wheeler, 1989). As such, we argue the dynamics of calcite precipitation (forming marl flats/tufa mounds/travertine deposits) and their relevance to ecosystem sustainability in calcareous fens is in need of further study.

Despite the prevalent down-valley hydraulic gradient in the Trough Fen, the lateral hydrological connection with the riparian swamp to the west was the key driver of pore-water nutrient patterns. Groundwater originating from the swamp and Fletcher Creek discharged at 60 cm depth in the area of the F1 and F4 nests, while there was a sustained small overland flow connection just north of the F4 nest and at the F5 nest (Chapter 3). These hydrological dynamics in the Trough hydrogeomorphic setting explain the decoupling of the biogeochemical cycles in the fen in relation to the flowpaths (Figure 4.6). The small groundwater inputs at F1 and F3 (as well as T1 in the Basin Fen) contained elevated nitrate (relative to the rest of the study fen areas) of 13 – 33 μg L^{-1}, most likely due to the lower DOC values (< 5 mg L^{-1}) along these flowpaths. The elevated nitrate in the F3 nest (> 20 μg L^{-1}) was most likely due to a higher redox potential (dissolved oxygen values were frequently ~3 mg $L\text{-}^{1}$) related to frequent water table drawdowns (Chapter 2).

The phosphate levels in the calcareous fen pore-water in the present study were on the low end of the range found previously in rich and calcareous fens in Europe (Boeye et al., 1995; Boyer and Wheeler, 1989; Lucassen et al., 2004a, 2006; Verhoeven et al., 1996; Wassen et al., 1990; Zak and Gelbrecht, 2007; Zak et al., 2009), though in the middle of the range reported in North America (Boomer and Bedford, 2008a; Komor 1994; Picking and Veneman, 2004; Vitt and Chee, 1990). Sites with similar or lower phosphate levels than the present calcareous fens all had very high iron concentrations, but lower pore-water calcium levels. Because of the high iron contents of the previous studies, the redox-sensitive iron biogeochemistry has been found to be a tighter control on phosphate availability than calcite dynamics (Boomer and Bedford, 2008b). Our results suggest that phosphate can be rendered unavailable even in the absence of appreciable iron in the peat and underlying strata, and that calcite dynamics act as controls. Beltman et al. (2000) have shown an increased concentration of phosphate may be due to exchange of chloride for phosphate on binding sites in fen peat; however, this was unlikely here as chloride levels averaged 58 mg L^{-1}, which was roughly half the level used in their experiments to produce the response.

The N:P ratio was very high across site, depth, and month, with the exception of the Trough Fen, which was only marginally above the critical value of 16 for plants (Koerselman and Meuleman, 1996). In contrast, the N:K ratio, and the availability of potassium was quite sufficient for normal plant functioning. The lower N:P in the least anoxic Trough Fen was more controlled by the very low ammonium availability than phosphate levels. Such high N:P ratios imply a very strong demand for bioavailable P, which presumably cannot be met by the sediment demand. Therefore, in calcareous and rich fens without appreciable iron content to participate in redox-mediated release of phosphate, the redox-insensitive calcite biogeochemistry becomes a very strong driver of PO_4^{3-}-limitation, as $CaCO_3$-PO_4^{3-} associations are very stable (Shenker et al., 2005).

There was significant seasonal variability in the available nutrients, suggesting studies grouping multiple sampling dates for averaging may miss some important linkages to fen ecology. The lowest phosphate levels were in July (Table 4.2). Maximum growth rates of many robust and slender herbaceous species occurred during this month. The dominant sedges undertook most of their seasonal growth in the early growing season, when P was relatively high and N was low (with the lowest N:P ratio). Fertilization increases sedge net primary productivity and P-storage (Chapin et al., 2004; Richardson and Marshall, 1986); however, it has been shown that low-P availability specifically drives high species richness in calcareous fens (Boyer and Wheeler, 1989; Boeye et al., 1997; Rozbrojová and Hájek, 2008). This suggests that calcareous fen sedge communities are adapted to the low-P conditions, and one mechanism of survival is through early-season growth when there is less competition for PO_4^{3-}.

Nitrate levels were extremely low in these fens, in stark contrast to the surface water levels, but did increase throughout the growing season, presumably due to the combination of higher stream stage, lack of plant demand, and an elevated redox status corresponding to water table drawdown farther from the stream source. In contrast, NH_4^+ levels were high relative to previous studies in calcareous fens (Lucassen et al., 2006; Verhoeven et al., 1996; Vitt and Chee, 1990), and were higher in the first half of the growing season and lower in the latter half, corresponding to a lower percentage of inorganic N as NH_4^+ (Table 4.2, Figure 4.8). It is possible that the high levels of divalent Ca^{2+} and Mg^{2+}, as well as Na^+, competed for cation binding sites with NH_4^+ in the peat and soil matrix, forcing NH_4^+ into solution (Lucassen et al., 2006), with the decreases later in the growing season attributable to either plant uptake or decreased net mineralization, as the base cation concentration did not vary systematically. The lower NH_4^+ and higher NO_3^- in July and August were coincident with a general decrease in PO_4^{3-} variability, especially the high concentrations (Figure 4.8). This artefact is attributable to one of two coupled processes; either maximum P-utilization from the pore-water is coincident with NH_4^+ utilization later in the season, or recreation of a redox buffer and/or increased nitrification lowers NH_4^+ build-up and prevents Fe^{3+} reduction-induced P-liberation.

Most calcareous and rich fen studies do not acidify water samples prior to the determination of PO_4^{3-}, as per standard colorimetry procedure (AWWA, 1998; Geurts et al., 2009; Koerselman et al., 1990; Lucassen et al., 2004; Vitt et al., 2009). However, several other authors have acidified pore-water samples prior to colorimetric PO_4^{3-} determination (Picking and Veneman, 2004; Shenker et al., 2005; Wassen and Joosten, 1996; Zak et al., 2009). Acidification is sometimes used to prevent metal precipitation (including bound phosphate, Banach et al., 2009; Carlyle and Hill, 2001). Our data demonstrate concentrations can differ by up to 30X between the two methods (Figure 4.2). Additionally, determination of phosphate via ion chromatography (Boyer and Wheeler, 1989) quantifies total dissolved phosphate, irrespective of complexation with calcium, iron, or other cations, while inductively coupled plasma atomic emission spectrometry (Drexler et al., 1999; Johnson and Steingraeber, 2003; Olde Venterink et al., 2002; Vitt and Chee, 1990) determines total phosphorus, including several forms unavailable to vegetation (Broberg and Pettersson, 1988). Thus, choice of methodology can impinge upon the interpretation of results.

Plants can only take up free, hydrogenated dissolved PO_4^{3-} (De Rijck and Schrevens, 1998; 1999). In slightly acidic to acidic conditions characteristic of moderate-rich and poor fens and bogs, nearly all of the dissolved PO_4^{3-} is in one of these forms (Dyśko et al., 2008). At higher pH values however, the PO_4^{3-} molecule becomes associated with Ca^{2+} and Mg^{2+} ions (Yao et al., 2001), rendering the dissolved P unavailable to plants. Our speciation calculations on the acidified samples indicate that in our calcareous fens up to 40 % of the determined PO_4^{3-} is not available at the pore-water pH (Figure 4.9). Ammonium incorporation into roots has been shown to lower rhizosphere pH by up to 0.6 units through the excretion of one H^+ ion (Li et al., 1991). Thus, even with this process (with the high NH_4^+ in the fen porewater) root zone pH would be expected to drop to only ~6.4. This drop in pH would convert some of the

$CaHPO_4$ to free HPO_4^{2-} or $H_2PO_4^-$ but there would still be a large store of unavailable $CaHPO_4$. Some agricultural plants have been shown to have a higher affinity for Ca-associated dissolved PO_4^{3-} (Zhu et al., 2002), but to our knowledge this has not been quantified for vegetation characteristic of calcareous fens. The variability in proportion of available PO_4^{3-} was strongly related to the saturation index of calcite, but this index is determined by the total pore-water chemical composition, and thus is not easily predicted in the field.

4.7 Conclusion

The majority of calcareous fen nutrient studies have focussed on the phosphate incorporated in the sediment fraction, with only cursory attention to the interstitial water. Those studies have revealed a strong dependence of iron biogeochemistry on P-liberation from the sediment. Our data from three calcareous fens with iron concentrations below detectable limits indicate that calcium carbonate biogeochemistry is equally effective in minimizing the availability of phosphate for plant uptake. High concentrations of dissolved calcium and magnesium prevented appreciable amounts of phosphate from being utilized by calcareous fen vegetation. Additionally, even with low iron levels, there was a redox buffer on nutrient availability, through denitrification, ammonification, and sulphate reduction. The hydrogeomorphic setting controlled the spatial patterns of dissolved constituents, as the redox gradients were coincident with the dominant hydrological flowpaths in the three fens of different landscape position. Removal of elevated nitrate concentrations in the source waters (stream and ground) was accomplished in short distance within the fen substrate. Redox conditions favourable for sulphate reduction occurred several metres beyond this zone of nitrate reduction, presumably due to low concentrations of electron donors. This study demonstrates that there exists substantial variability in biogeochemical functioning not only between calcareous fens, but also within a site, and spatial patterning of species richness may be controlled by the coupling of biogeochemical cycles.

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Table 4.1: Effect of site (Riparian West and East, Trough, and Basin Fen), depth (upper peat, lower peat, mineral), and growing season month (May, June, July, August) on pore-water nutrient concentrations. Acid PO_4^{3-}P refers to concentrations determined on acidified samples; PO_4^{3-}-Ratio refers to ratio of acidified to unacidified phosphate values; N:P and N:K ratios are molar ratios; % N as NH_4^+ refers to inorganic N only. Values are F-ratios with level of significance from three-way ANOVA.

Source of Variation	df	PO_4^{3} P	Acid-PO_4^{3-}-P	PO_4^{3-}-Ratio	NO_3^--N	NH_4^+-N	K^+	N:P	N:K	%N as NH_4^+
Site	3	4.01^{**}	12.08^{***}	6.88^{***}	2.54	29.36^{***}	132.33^{***}	18.38^{***}	35.47^{***}	12.43^{***}
Depth	2	0.74	0.08	0.26	1.74	5.91^{**}	11.40^{***}	3.68^{*}	3.42^{*}	2.30
Month	3	5.32^{**}	0.61	1.21	8.32^{***}	1.94	3.57^{*}	3.51^{*}	2.26	2.60
Site x Depth	6	0.88	1.11	0.43	3.69^{**}	2.60^{*}	10.68^{***}	2.73^{*}	2.06	1.42
Site x Month	9	2.76^{**}	0.77	0.90	2.56^{*}	0.47	1.02	0.76	0.59	1.57
Depth x Month	6	0.32	0.33	0.29	1.00	0.37	0.26	0.37	0.59	0.72
Site x Depth x Month	18	0.37	0.40	0.48	0.83	0.21	0.19	0.34	0.28	0.66

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 4.2: Mean pore-water nutrient concentrations grouped by site, depth, and month as in Table 4.1. Different letters within each nutrient-group section represent significant differences ($P \leq 0.05$) using Tukey's HSD Test.

	PO_4^{3-}-P (µg L^{-1})	NO_3^--N (µg L^{-1})	NH_4^+-N (µg L^{-1})	K^+ (mg L^{-1})	N:P ~	N:K ~	%N as NH_4^+ (%)
Site:							
Riparian West	11.0^{ab}	13.0^{a}	216.8^{ab}	2.63^{a}	58.24^{ac}	0.24^{a}	92.3^{a}
Riparian East	12.4^{b}	27.0^{a}	808.1^{b}	1.13^{b}	133.86^{a}	1.78^{b}	91.4^{a}
Trough	9.5^{a}	19.6^{a}	56.0^{c}	0.86^{b}	19.64^{b}	0.29^{a}	77.1^{b}
Basin	11.7^{ab}	9.4^{a}	161.6^{a}	0.61^{c}	34.67^{c}	0.88^{b}	91.6^{a}
Depth:							
Upper Peat	11.5^{a}	18.8^{a}	404.7^{a}	1.41^{a}	77.64^{a}	0.74^{a}	90.2^{a}
Lower Peat	11.2^{a}	16.6^{a}	359.0^{a}	1.26^{b}	68.96^{ab}	1.08^{a}	87.8^{a}
Mineral	10.4^{a}	16.9^{a}	109.5^{b}	1.14^{b}	28.53^{b}	0.45^{b}	83.7^{a}
Month:							
May	11.9^{a}	10.0^{a}	235.2^{a}	1.28^{ab}	36.48^{a}	0.57^{a}	88.6^{a}
June	10.1^{ab}	11.7^{a}	348.9^{a}	1.42^{b}	70.52^{b}	0.69^{a}	92.4^{a}
July	9.8^{b}	18.1^{b}	293.9^{a}	1.12^{a}	76.36^{b}	0.86^{a}	82.3^{a}
August	12.2^{a}	29.9^{b}	286.1^{a}	1.27^{ab}	50.15^{b}	0.91^{a}	85.6^{a}

Table 4.3: Correlation coefficients of calcareous fen pore-water chemistry across all sites and full growing season.

	PO_4^{3-}-P	NO_3^--N	NH_4^+-N	Cl^-	Ca^{2+}	Mg^{2+}	K^+	Na^+	SO_4^{2-}	%N as NH_4^+	N:P	N:K	pH	EC	DOC
PO_4^{3-}-P	x														
NO_3^--N	~	X													
NH_4^+-N	0.52^{**}	~	x												
Cl^-	0.15^{***}	~	~	x											
Ca^{2+}	~	~	~	~	x										
Mg^{2+}	0.22^{***}	~	~	-0.11^{*}	0.38^{***}	x									
K^+	~	~	0.17^{**}	~	~	-0.26^{***}	x								
Na^+	0.41^{*}	~	0.17^{**}	0.13^{*}	~	~	~	x							
SO_4^{2-}	~	~	~	~	0.19^{*}	~	~	-0.43^{***}	x						
%N as NH_4^+	0.31^{***}	-0.64^{***}	0.29^{***}	~	0.13^{**}	~	0.33^{***}	~	~	x					
N:P	~	~	0.91^{***}	-0.15^{**}	~	~	0.22^{***}	0.14^{**}	~	0.27^{***}	x				
N:K	0.53^{***}	~	0.84^{***}	~	~	0.12^{*}	~	0.17^{***}	~	0.19^{***}	0.76^{***}	x			
pH	~	~	~	~	~	-0.55^{***}	0.20^{*}	~	~	~	~	-0.24^{*}	x		
EC	~	~	~	~	0.70^{***}	0.70^{***}	~	~	~	~	~	~	-0.33^{***}	x	
DOC	~	~	~	-0.18^{**}	~	-0.42^{***}	-0.15^{**}	-0.34^{***}	0.39^{***}	~	~	~	-0.64^{***}	~	x

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ~ = non-significant correlation

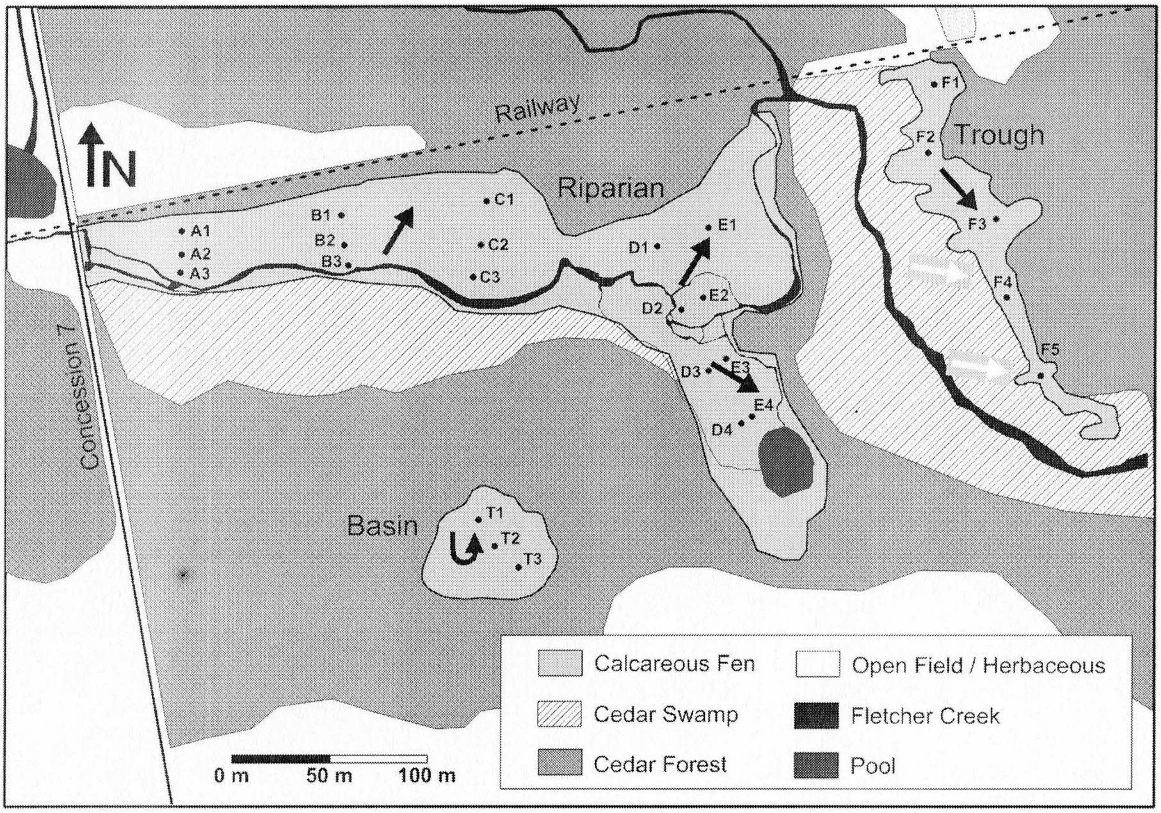


Figure 4.1: Location of the calcareous fen study sites. Dots and labels indicate piezometer sample nests. Arrows indicate principal water flowpaths: black arrows represent subsurface flow; curved arrow groundwater upwelling; and white arrows overland flow connection.

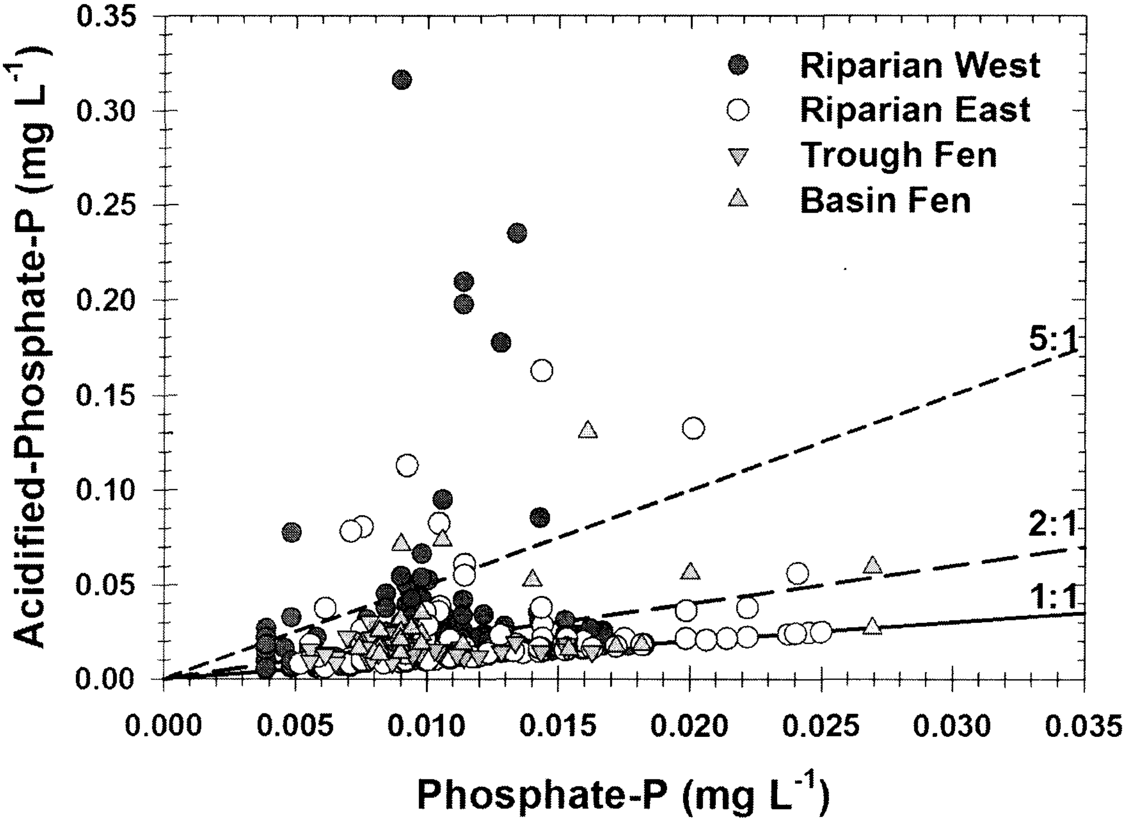


Figure 4.2: Variability in overestimation of bioavailable pore-water phosphate through acidification of samples.

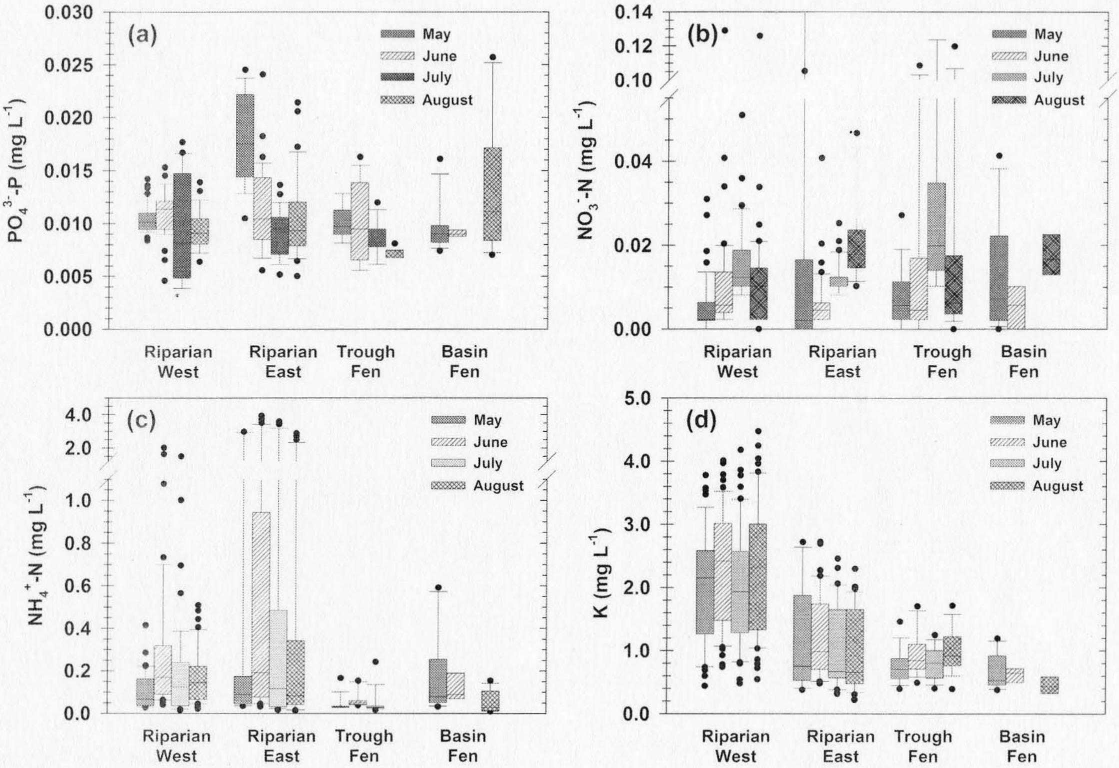
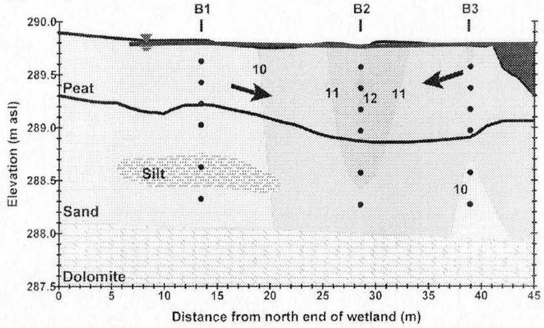
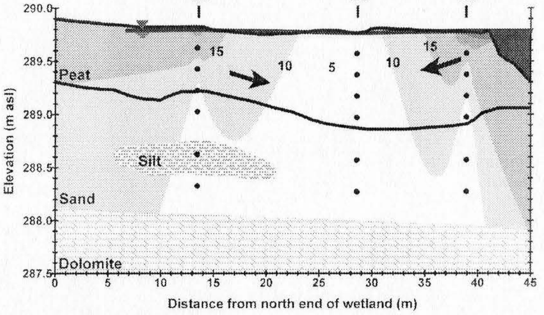


Figure 4.3: Site and seasonal variability in pore-water nutrients depicting (a) phosphate, (b) nitrate, (c) ammonium, and (d) potassium concentrations.

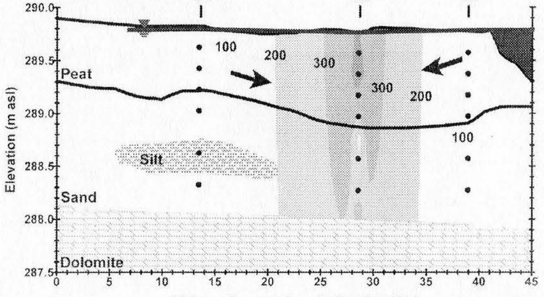
(a) Phosphate-P



(b) Nitrate-N



(c) Ammonium-N



(d) Sulphate

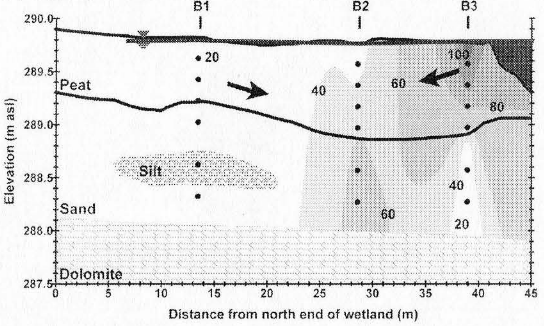
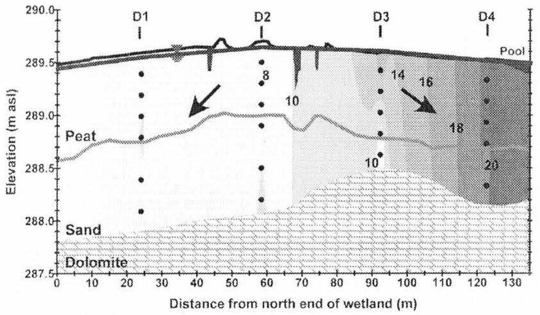
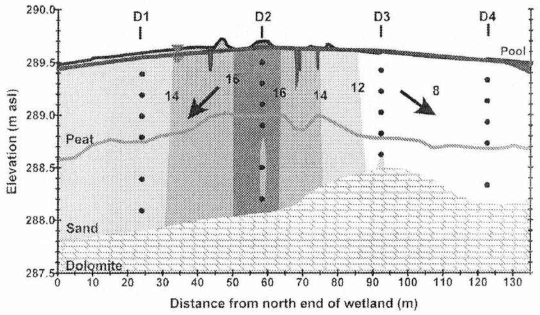


Figure 4.4: Spatial variation in pore-water redox-sensitive elements in the Riparian West Fen: (a) phosphate-P (μg L^{-1}); (b) nitrate-N (μg L^{-1}); (c) ammonium-N (μg L^{-1}); and (d) sulphate (mg L^{-1}). Isoline interval is 1, 5, 100 μg L^{-1}, and 20 mg L^{-1} for (a-d), respectively. Arrows represent dominant hydraulic gradient during sampling period. Vertical exaggeration is 10X.

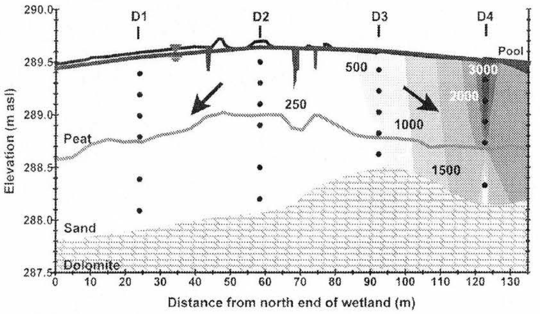
(a) Phosphate-P



(b) Nitrate-N



(c) Ammonium-N



(d) Sulphate

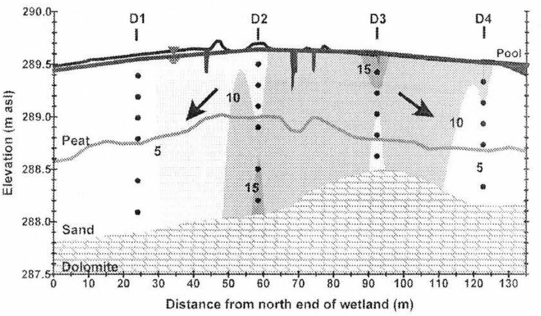
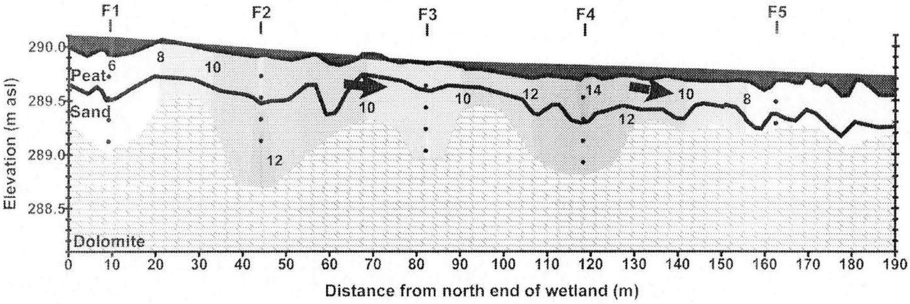
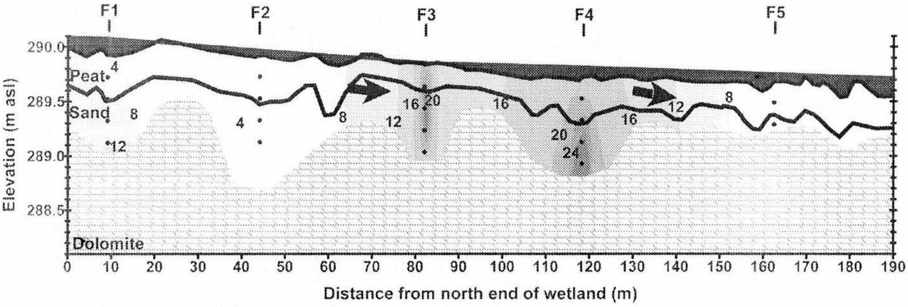


Figure 4.5: Spatial variation in pore-water redox-sensitive elements in the Riparian East Fen: (a) phosphate-P ($\mu g\ L^{-1}$); (b) nitrate-N ($\mu g\ L^{-1}$); (c) ammonium-N ($\mu g\ L^{-1}$); and (d) sulphate ($mg\ L^{-1}$). Isoline interval is 2, 4, 500 $\mu g\ L^{-1}$, and 5 $mg\ L^{-1}$ for (a-d), respectively. Arrows represent dominant hydraulic gradient during sampling period. Vertical exaggeration is 30X.

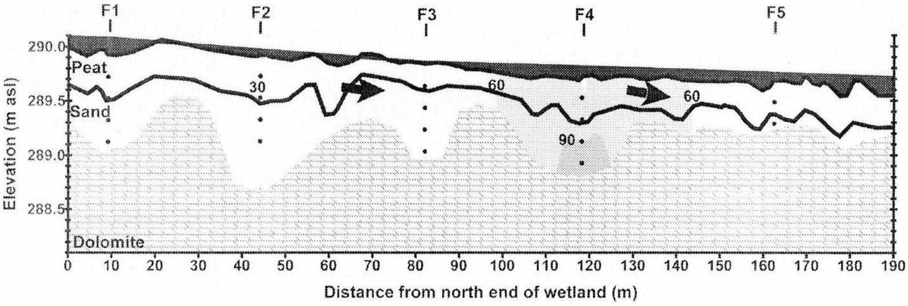
(a) Phosphate-P



(b) Nitrate-N



(c) Ammonium-N



(d) Sulphate

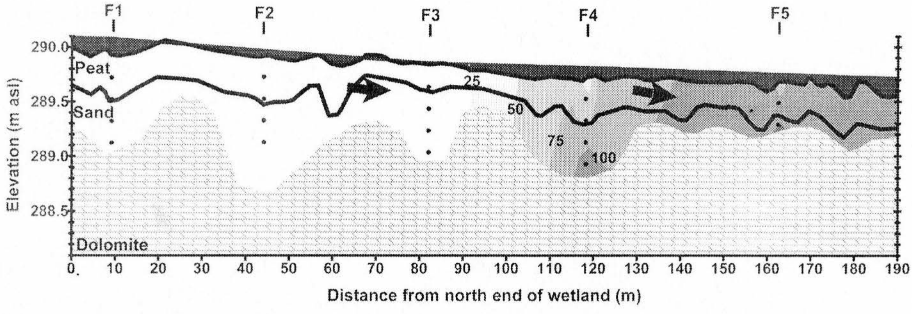
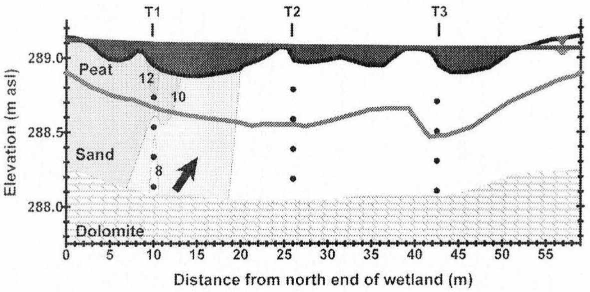
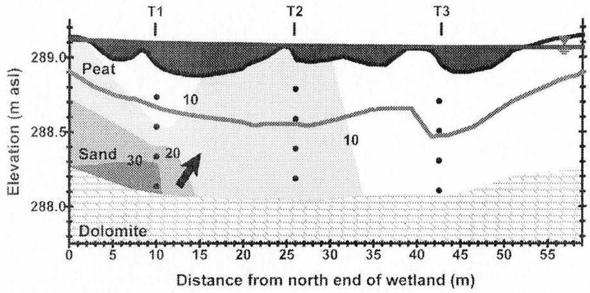


Figure 4.6: Spatial variation in pore-water redox-sensitive elements in the Trough Fen: (a) phosphate-P ($\mu g\ L^{-1}$); (b) nitrate-N ($\mu g\ L^{-1}$); (c) ammonium-N ($\mu g\ L^{-1}$); and (d) sulphate ($mg\ L^{-1}$). Isoline interval is 2, 4, 30 $\mu g\ L^{-1}$, and 25 $mg\ L^{-1}$ for (a-d), respectively. Arrows represent dominant hydraulic gradient during sampling period. Vertical exaggeration is 25X.

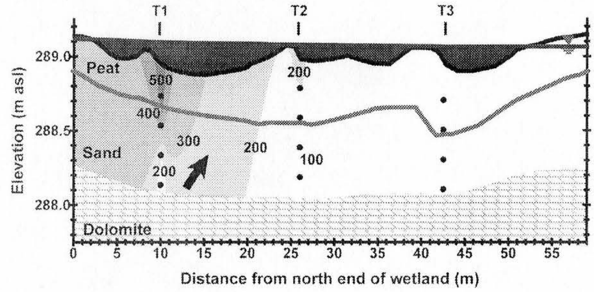
(a) Phosphate-P



(b) Nitrate-N



(c) Ammonium-N



(d) Sulphate

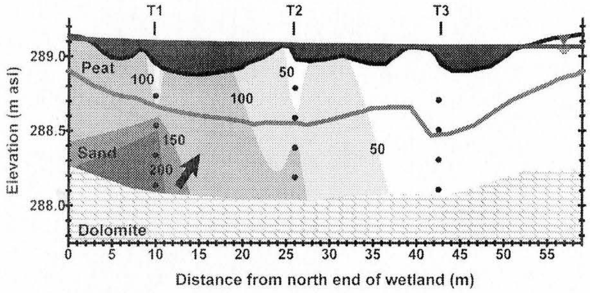


Figure 4.7: Spatial variation in pore-water redox-sensitive elements in the Basin Fen: (a) phosphate-P (μg L^{-1}); (b) nitrate-N (μg L^{-1}); (c) ammonium-N (μg L^{-1}); and (d) sulphate (mg L^{-1}). Isoline interval is 2, 10, 100 μg L^{-1}, and 50 mg L^{-1} for (a-d), respectively. Arrow represents dominant hydraulic gradient during sampling period. Vertical exaggeration is 16X.

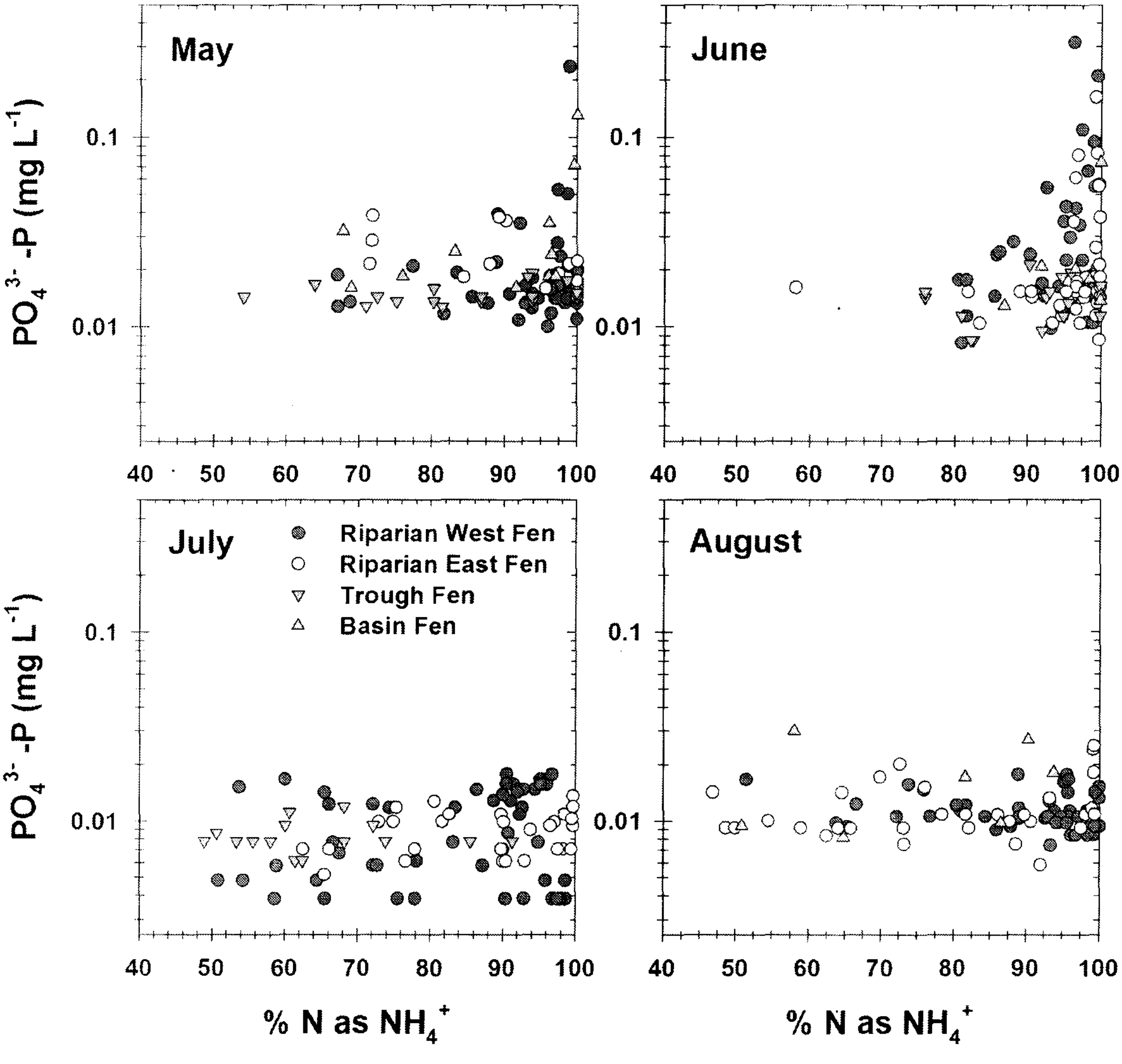


Figure 4.8: Seasonal progression of pore-water phosphate concentration in relation to the percentage of inorganic nitrogen present as ammonium across the calcareous fens.

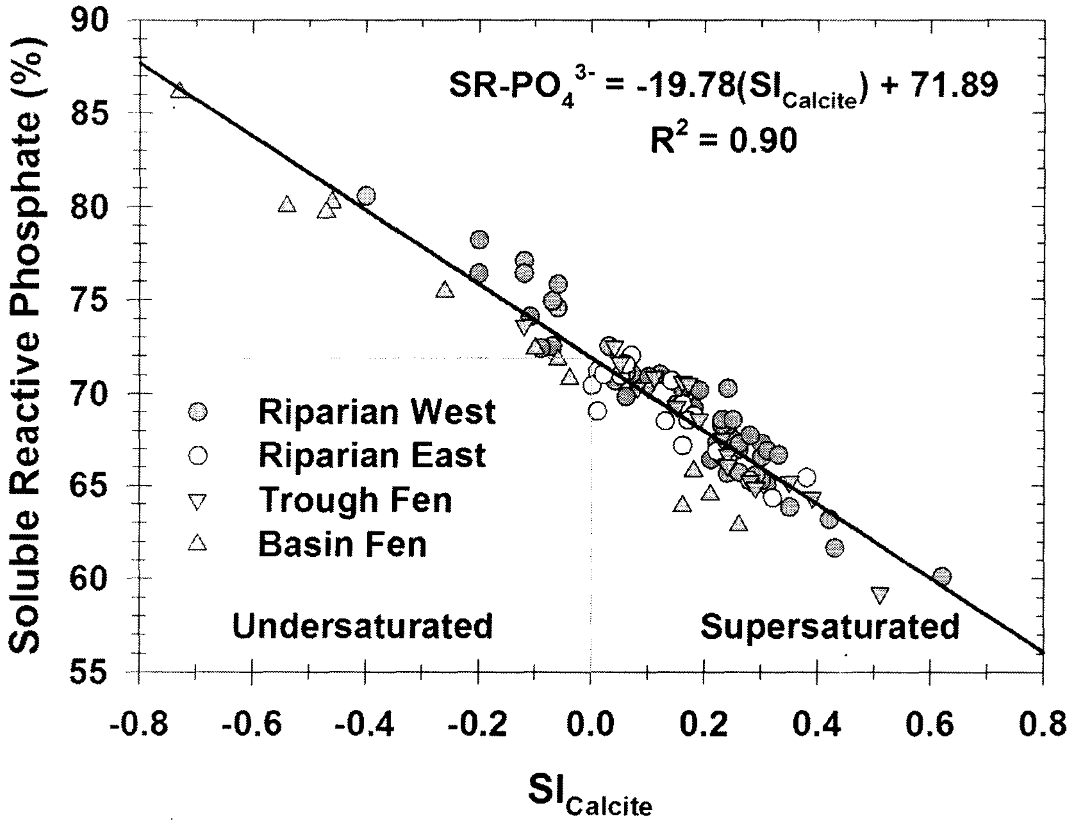


Figure 4.9: Percent of pore-water phosphate readily available for plant uptake (as HPO_4^{2-} and $H_2PO_4^-$) as a function of the pore-water saturation index of calcite.

CHAPTER 5:
HYDROLOGICAL AND BIOGEOCHEMICAL CONTROLS ON PLANT SPECIES DISTRIBUTION WITHIN CALCAREOUS FENS

5.1 Abstract

Calcareous fens are wetland ecosystems of very high species richness and diversity; however, the direct causes of their biodiversity have rarely been investigated in detail. This study determines spatial patterns of plant species richness and diversity in three calcareous fens of southern Ontario, Canada, in relation to a suite of environmental variables and quantifies individual species response and range/tolerance to hydrological, peat physical, and pore-water nutrient gradients using non-linear quantile regression. Species richness and diversity were highly variable across the sites, with no single species occupying greater than 25 % of the area surveyed. Hydrological regime was also highly variable across the fens and was related to distance from a second order stream. Surface peat organic matter and calcium carbonate content ranged from 11 to 91 % and 2 to 83 %, respectively. Dissolved inorganic nitrogen and potassium concentrations from the shallow pore-water ranged from 0 to 4 mg L^{-1}, whereas available phosphorus was < 100 $\mu g\ L^{-1}$. Individual species exhibited various response shapes to the environmental gradients, which produced drastically variable and segregated realized ranges. The duration of initial growing season saturation and the surface peat organic matter content produced the most functionally useful species responses. Aggregation of species across growth types (sedges, herbs, grasses, shrubs) based on environmental responses mirrored visually described communities, demonstrating the applicability of the method of analysis. The generation of species response curves for a suite of readily measured environmental variables can be a useful tool for assessing conceptual models of ecosystem functioning and wetland restoration/creation success.

5.2 Introduction

Calcareous fens are wetlands fed principally by water rich in calcium, magnesium, and bicarbonate (Almendinger and Leete, 1998b; Komor, 1994), have accumulated more than 40 cm of peat (Mitsch and Gosselink, 2007; National Wetlands Working Group, 1997), and have near-surface soil and surface water pH in the range of 6.0 to 7.8 (Bedford and Godwin, 2003; Eggers and Reed, 1987). Dominated by sedges and brown mosses, calcareous fens exhibit very high vascular and non-vascular plant species richness and diversity (Motzkin, 1994; Wheeler, 1988), serve as regional refugia for a number of rare plant taxa (Amon et al., 2002; Bowles et al., 2005a) and are a focus of conservation and restoration efforts for these biodiversity values (Cooper and MacDonald, 2000; Lamers et al., 2002; Middleton et al., 2006). Plant species richness and diversity are higher in calcareous fens than other fens due to the associated peat and pore-water biogeochemistry along the poor-rich fen gradient (Johnson and Steingraeber, 2003; Nekola, 2004; Rozbrojová and Hájek, 2008; Vitt and Chee, 1990), particularly the scarcity of inorganic phosphorus (Lucassen et al., 2004; Olde Venterink et al., 2001;

Wassen et al., 1990). In this study, however, we investigate the environmental controls of within-fen plant richness and diversity, which have received less attention.

Calcareous fens are presumed to form at local sites of alkaline groundwater discharge, and it has been shown that a transition of plant species occurs with increasing distance from these seepage points (Wheeler, 1980). However, the plant diversity is not common in all landscapes. Several studies have demonstrated that plant species richness, diversity, and rarity are maximized at these groundwater springs (Boyer and Wheeler, 1989; Gilvear et al., 1993; Miner and Ketterling, 2005). This finding is far from ubiquitous, as several other studies purport seepage sites, commonly referred to as marl flats or tufa mounds, are stressful for vascular growth, and subject to very low richness and biomass (Bowles et al., 2005b; Cooper, 1996; Johnson and Steingraeber, 2003).

Other studies have demonstrated that within-site variability in hydrological regime, such as water table fluctuation, water table drawdown, and flooding duration, elicit significant change in plant species composition (Hájková et al., 2004; Nekola, 2004), even though maintenance of the water table near the ground surface is one of the prime tenets of calcareous fen ecosystem functioning (Almendinger and Leete, 1998b; Amon et al., 2002; Bedford and Godwin, 2003; Mitsch and Gosselink, 2007). Recently, we have shown that there exists tremendous variability in the hydrological regime of calcareous fens, including water table dynamics (Chapter 2), water balance components, and subsurface flowpaths (Chapter 3), in addition to nutrient biogeochemistry (Chapter 4). Therefore, there remain questions about the controls on within-site plant species distribution in calcareous fens. Such knowledge will aid management decisions for the preservation and restoration of these valuable ecosystems through formulation of process-based targets for plant species success.

Traditional approaches for quantifying the of controls on individual plant species range and community distribution, including correlation regression and multivariate correspondence analysis (Johnson and Steingraeber, 2003; Nekola, 2004; Picking and Veneman, 2004), assume either a linear relationship between the dependent and independent variable(s) or a Gaussian bell-shaped response (Oksanen and Minchin, 2002). These approaches have prevailed despite it long being recognized that species response to environmental gradients are inherently non-linear (Austin, 1976), and often are not adequately described by the Gaussian model (Austin, 1999). Furthermore, the use of standard correlation approaches using the conditional means of natural field datasets disregard the basic ecological concept of limiting factors (Thomson et al., 1996). That is, minimization of the residuals about the mean response of a dependent variable (species cover) to an independent variable (environmental gradient) by definition excludes the upper and lower bounds on the response variable. One fruitful approach to overcoming this conflict is through the use of quantile regression, particularly the upper quantiles, which does a much better job representing the constraints imposed on one variable from another (Cade and Guo, 2000; Cade et al., 1999; Krause-Jensen et al., 2000; Scharf et al., 1998). Recently, Schröder et al. (2005) have combined regression of the 95th-quantile with the asymmetric non-linear logistic response functions of Huisman et al. (1993), which is a promising approach to the realistic depiction of species response to environmental gradients (Austin, 2007). The riparian fen ecosystem studied by Schröder et al. (2005) was characterized by several near-monotypic stands. It remains to be seen if non-linear quantile regression can detect plant species responses to environmental gradients in settings such as calcareous fens with high species diversity with low individual species cover.

In this study we adopt the approach of Schröder et al. (2005) to investigate the environmental controls on within-site species richness and diversity in three calcareous fens located within a wetland complex. Determination of the key controls on species distribution within calcareous fens is crucial for effective conservation, restoration, and creation of these wetland systems that have a high ecological value in a region (Moran et al., 2008). Specifically we address the following questions:

(1) How do plant species richness and diversity vary across a calcareous fen?
(2) How do environmental, including hydrological, peat physical, and pore-water chemical, gradients vary within calcareous fens?
(3) How do individual plant species respond to environmental gradients present in calcareous fens, and is non-linear quantile regression capable of detecting these responses?
(4) Which hydrological and biogeochemical gradients elicit the greatest control on plant species range?

5.3 Methods

5.3.1 Study Sites

The three calcareous fens are located in a 332 ha headwater catchment of the Spencer Creek Watershed, 70 km west of Toronto, Ontario, Canada (Figure 5.1). The catchment spans 50 m of elevation, from 337 to 287 m above sea level and is underlain by fractured dolomite of the Guelph Formation (Upper Silurian in age). The northern half of the catchment contains 0 – 25 m of glacial till derived from the Galt Moraine northwest of the catchment. The till grades into outwash fine sands and silts at the northern boundary of the fens. The southern half of the catchment contains no glacial overburden and soils range from 0 – 60 cm thick. Upland vegetation consists primarily of *Thuja occidentalis* L. and *Betula papyrifera* Marsh. thickets interspersed by grass and shrubland. A series of groundwater seeps emerge mid-way down the catchment, which coalesce in a cedar swamp to form a clear, cold-water stream. This stream, Fletcher Creek, then flows through one of the calcareous fens, followed by a cedar swamp, then a cattail marsh at the outlet of the catchment.

The three fens are named according to their hydrogeomorphic position: Riparian Fen, Trough Fen, and Basin Fen (Figure 5.1). The Riparian Fen is gently sloping, with only 30 cm elevation change across 450 m of stream length (stream gradient of 0.00067). A small pool occupies the southern-most portion, which is surrounded by calcite precipitate known as a marl flat (Miner and Ketterling, 2005). The Trough Fen is bordered on the east by an upland thicket of cedar trees and to the west and south by a riparian cedar swamp. The minimum distance from the edge of the Trough Fen to Fletcher Creek is 20 m at points at the northernmost, middle, and southernmost portions of the fen. Elsewhere, the fen is separated from the stream by 40-75 m of riparian swamp. There is 43 cm of elevation change along the 200 m length of the wetland. The Basin Fen occupies a gentle depression in the upland cedar forest. There is at least 100 m of cedar upland or cedar swamp between the Basin Fen and Fletcher Creek, with no surface connection. Elevation of the fen floor varied by only 15 cm; however, the formation of tussocks of peat up to 70 cm above this fen floor by *Carex stricta* led to a highly variable surface topography.

5.3.2 Field Methods

We used a stratified sampling strategy to ensure an inventory of all visually distinct vegetation communities. A total of 141 0.5 X 0.5 m quadrats were sampled at 5 m intervals along eight transects in the three calcareous fens in July 2006 (Figure 5.1). Percentage cover was visually recorded for all vascular plants to the species level, bryophytes, bare ground, and water. Voucher specimens of rare and/or difficult to identify species were placed in the University of Toronto at Mississauga Herbarium. To relate plant species distribution to fen hydrologic regime a series of groundwater wells (see Chapter 2 for details) were installed adjacent to the sampling transects. Water level was recorded approximately weekly throughout the growing season in each well. Upon completion of the vegetation survey, a 10 cm X 10 cm monolith of the surficial 20 cm of peat was carefully extracted from the centre of each quadrat for further analysis in the laboratory. Pore-water was allowed to fill the pit in each quadrat, whereupon a sample was collected in a sample cup for field determination of pH and specific conductance. A second sample was collected in a 50 mL polypropylene container and placed on ice for further analysis in the laboratory. The depth of peat in each quadrat was measured by inserting a 2 m piece of rebar until meeting resistance.

5.3.3 Soil and Water Analysis

The peat monoliths were weighed, oven dried at 70 °C until constant weight, and reweighed for determination of field moisture content and bulk density. Each oven-dried monolith was homogenized and a subsample was used for the determination of organic matter and calcium carbonate content through loss-on-ignition at 550 °C for four hours and 950 °C for two hours, respectively. Collected water samples were filtered through 0.45 μm cellulose membrane filters upon return to the lab and frozen until analysis for nutrients. Total dissolved inorganic nitrogen was determined as the sum of nitrate and ammonium on a Technicon® auto-analyzer colorimeter using the sulphanilamide following cadmium reduction and the Berthelot methods, respectively (Environment Canada, 1979). Available phosphorus was determined as soluble reactive phosphate using the molybdate blue method colormetric method (Environment Canada, 1979). Minimum detection limits for NH_4^+-N, NO_3^--N, and PO_4^{3-}-P were 8, 4, and 2.5 μg L^{-1}, respectively. Accuracy for NH_4^+-N, NO_3^--N, and PO_4^{3-}-P was determined to be 1 %, 2 %, and 5 %, respectively, in the range of sample concentration. Potassium was determined on a Perkin Elmer® Aanalyst 400 atomic absorption spectrometer. Analytical accuracy was 0.02 ppm and minimum detection limit was 0.01 ppm.

5.3.4 Data Analysis

Plant species richness was calculated as the total number of vascular species per quadrat and site. Species diversity of each quadrat and site was calculated using the Shannon-Wiener Index of Diversity:

$$H = - \Sigma\, p_i \ln (p_i), \qquad [1]$$

where p_i is the proportion cover of total number of species made up of the ith species. Sørensen's Coefficient of Similarity was calculated between sites. Three metrics of hydrology were chosen to evaluate plant species response: duration of initial saturation; percentage of growing season subject to saturation; and, total growing season water table amplitude (range). These metrics were chosen over more traditional hydrologic metrics (such as mean and median), as they are more capable of causing a direct effect on plant species growth and survival (Bernard, 1990; Chapter 2; Schröder et al., 2005). Linear interpolation and extrapolation between groundwater monitoring wells was used to assign a value of each water level sampling date to each sampled quadrat. All three calcareous fens were completely saturated at the onset of the growing season, with differential water table drawdowns: the timing of this drawdown was used as the duration of initial saturation. The spatial distributions of measured and calculated variables were estimated through semi-variograms using the Kriging method of interpolation in Surfer 7® (Golden Software, 1999). Pearson correlation coefficients between all measured variables were calculated in SYSTAT 12® (SYSTAT, 1997).

The response of individual species to environmental gradients across the calcareous fens was modelled using logistic growth functions (Huisman et al., 1993; Oksanen and Minchin, 2002):

$$y = M \frac{1}{1+e^{a+bx}} \frac{1}{1+e^{c-dx}}, \qquad [2]$$

where y is the species response (percent cover) and x is the explanatory environmental gradient eliciting the response. The parameters to be estimated are a, b, c, and d. In the logistic growth model M represents the maximum value that y can reach; therefore, M was set to 100 (assuming an individual species can attain 100 % coverage in a quadrat). This non-linear growth function was applied to the 95th quantile of the point cloud of each plant species' percentage cover against each environmental variable used in the analysis. The statistical computation was performed in STATISTICA® using the user-defined function above in the non-linear regression package with the user-defined asymmetric loss function provided in the Appendix of Schröder et al. (2005). If parameters b and d had the same sign after fitting the growth function, both describing the same direction of change in the species response, the calculation was re-run with parameter d set to zero. A total of 24 species were selected for modelling, six each from the following classes: true sedges of the Carex genus, herbaceous species, grasses and sedge allies (belonging to the *Cyperaceae* family), and shrubs. Each species selected was present in at least 10 % of the sampled quadrats and represented at least 1 % of the total cover of vascular vegetation across all three of the study fens.

If the modelled plant species response function produced a slope equal to zero, approximating a maximum of species cover for the measured range of that environmental variable, an estimation of the range or tolerance of the species to that variable was made. This range or tolerance was calculated as the part of the response function where the predicted (modelled) species cover exceeded 50 % of the maximum predicted cover. The non-linear response function did not produce a zero-slope/maximum for some species in the measured range of some environmental variables: in these instances no species range could be calculated.

5.4 Results

5.4.1 Plant Species Richness and Diversity

We identified 103 vascular species across the three sites (Appendix 5.1). No species represented more than 25 % of the vegetation of any of the sites. Of these species, nearly one third (29) belonged to the *Cyperacaeae* family, including 19 varieties of *Carex spp.* None of the sites had more than 65 plant species present, and Sørensen's Coefficient confirms the relative lack of commonality between the sites, with the Trough and Basin Fens being the most closely related (Table 5.1). Hydrological and geochemical evidence (Chapters 2-4) suggest the west and east halves of the Riparian Fen are distinct, and were separated for this analysis. The diversity of the species present was much higher in the Riparian West site than the Riparian East site, with the Trough and Basin Fens intermediary (Table 5.1).

Across the sites, plant species richness within a 0.25-m^2 quadrat was highly variable (Figure 5.2a). In general, 13 species per quadrat were identified in the Riparian West site, with local highs of 17 to 22 adjacent to the stream. In contrast, the Riparian East site was characterized by fewer species per quadrat, with most of the site having fewer than 10 species per quadrat, with the extreme of the southern half consisting only of *Carex aquatilis* and *Lysimachia thrysiflora*, and occasionally *Eleocharis eyrthropoda* (Figure 5.2a). The Trough Fen contained greater number of species in the northern half of the fen, reaching densities of 26 per quadrat, and low numbers in the upper- and lower-middle portions. The Basin Fen had ~10 species per quadrat, with localized increases of 16-17 associated with tussocks.

In general, plant species diversity decreased with increasing distance from the second order Fletcher Creek (Figure 5.2b). The exception to this pattern was the south half of the Riparian East site, where low richness and the dominance of the robust *C. aquatilis* resulted in very low diversity. A band of diversity values > 2.5 extended from the stream in the Riparian West site north-east through the Riparian East site, continuing into the northern section of the Trough Fen. The majority of the Trough Fen was characterized by a Shannon-Wiener Index of ~1.5, with local peaks >2.0. Species diversity mirrored species richness in the Basin Fen, where values were generally ~1.5 except for localized peaks >2.0 associated with the sampling of tussocks (Figure 5.2b).

Not surprisingly, plant species richness and diversity were strongly correlated ($R^2 = 0.84$, $p<0.001$, Table 5.2); however, there were very few correlations with the measured environmental variables. Calcium carbonate content was the strongest correlation with both richness and diversity: increasing $CaCO_3$ content led to lower biodiversity (Table 5.2). Increasing organic matter generally was significantly but weakly correlated with higher richness and diversity ($R^2 = 0.24$ and 0.29, respectively, both $p<0.001$). Peat depth was strongly negatively correlated with water table amplitude, as was pore-water potassium content ($R^2 = -0.6$, $p<0.001$). All three hydrologic variables, peat composition, and phosphorus and potassium levels were all correlated with each other and pH and conductivity of the pore-water and surface moisture content, though to varying degrees. Dissolved inorganic nitrogen was only correlated with pore-water specific conductance ($R^2 = -0.23$, $p<0.05$). From this analysis we chose nine of the 13 measured environmental variables (numbers 5 – 13 in Table 5.2) representing hydrological and biogeochemical gradients in calcareous fens for further examination of individual species response.

5.4.2 Environmental Gradients

Most of the streamside area of the Riparian Fen was subject to constant saturation and/or flooding for at least the first 20 weeks of the growing season (until the last 2 weeks of August) (Figure 5.3a). This zone of direct influence of the stream extended for approximately 20 m inland. In contrast, portions of the Riparian West Fen became unsaturated after just 3.5 weeks into the growing season (early-mid May). The southern portion of the Trough Fen had standing water for the first 20 weeks of the growing season, whereas the middle portions were only continuously saturated for ~10 weeks. At just 0.45 ha the Basin Fen was still subject to vastly different timing of water table drawdown, ranging from eight to 20 weeks of continuous saturation (Figure 5.3a).

Despite the variable water table fluctuation observed to start the growing season, the Basin Fen was still subject to standing water for > 80 % of the total growing season (Figure 5.3b). Likewise, the distributaries of Fletcher Creek in the southern portion of the Riparian Fen also led to saturation of the peat for > 80 % of the growing season, as did several streamside areas. However, portions of the northern Riparian Fen and the middle of the Trough Fen were only saturated for 15-30 % of the growing season.

Water table amplitude of less than 10 cm occurred in the immediate 10 m of streamside peat (Figure 5.3c). A zone of 10-20 cm fluctuation extended an additional 0-45 m from the stream, with amplitude reaching > 50 cm 50 m from the stream. Portions of the Trough Fen closest to Fletcher Creek (north and south portions) also experienced smaller amplitudes. Areas > 60 m from the stream, (Basin Fen and middle of Trough Fen) experienced > 60 cm water table amplitude (Figure 5.3c).

Organic matter content of the surficial peat ranged from less than 10 % in the calcified sediments of the marl flat in the Riparian Fen to > 90 % in portions of each of the fens (Figure 5.4a). The areas of highest organic matter content included the consistently flooded Basin Fen, the near-stream areas of the Riparian Fen, and the north and south portions of the Trough Fen. While there was a significant inverse relationship between organic matter content and calcium carbonate content (Table 5.2), especially in the marl flat, there were areas, such as the northern-most and middle portions of the Trough Fen, where moderate calcium carbonate concentrations were mixed with predominantly organic soils (Figure 5.4a,b). While the surface peat of the Basin Fen was largely devoid of calcium carbonate, very high levels were present at >25 cm depth (Duval, unpublished data). Bulk density was very low across the surface peat of the calcareous fens, especially the Riparian East and Basin Fens, but generally increased with increasing distance from the stream in the Riparian West Fen (Figure 5.4c). The bulk density of the Trough Fen was very heterogeneous with isolated pockets of very loose material and relatively denser surficial sediments.

Total dissolved inorganic nitrogen reached concentrations of greater than 4 mg L^{-1} in the shallow pore-water, and was composed predominantly of either ammonium (majority of locations in Riparian and Basin Fens) or nitrate (Trough Fen, data not shown). Lowest concentrations of DIN were found in near-stream sediments and throughout the Trough Fen (Figure 5.5a). Peak DIN values were found in the marl flat and pockets of the Basin Fen. Bioavailable phosphate was generally very low throughout the fens, particularly the Trough Fen, where levels were < 20 μg P L^{-1} (Figure 5.5b). Near-stream shallow pore-water generally contained < 20 μg L^{-1} as well, except for the west and east margins. A few samples in the southern portion of the Basin Fen contained > 70 μg P L^{-1}. The Riparian Fen pore-water potassium levels were much higher than the other two sites, with concentrations between 2 and 4.5 mg L^{-1}, largely invariant to proximity to the stream (Figure 5.5c). Trough Fen potassium levels decreased downgradient from 2 to < 0.5 mg L^{-1}, while there was an isolated area of the Basin Fen with elevated levels (Figure 5.5c).

5.4.3 Plant Species Response and Range to Environmental Gradients

All 24 plant species analyzed showed a response to increasing duration of initial saturation (Figure 5.6a). Some species, such as *Carex aquatilis*, *Lycopus uniflorus*, and *Muhlenbergia glomerata* increased their percentage cover with increasing continuous saturation, without reaching maximum cover within the measured range. On the other hand prolonged initial saturation led to decreasing cover of *Eupatorium maculatum*, *Solidago uliginosa*, and *Cornus stolonifera*. Some species displayed a unimodal response to the timing of initial water table drawdown, such as *C. aquatilis*, *C. lacustris*, and *C. livida*, which peaked at different durations, but had significant overlap (Figure 5.6a). The herbs *Mentha arvensis* and *Menyanthes trifoliata* also had unimodal distributions, but without overlapping cover. *Rhamnus alnifolia* and *Typha spp.* peaked at opposite ends of the measured gradient, confirming the lack of co-existence.

Most of the species tested were not as responsive to total duration of growing season saturation as the initial duration, particularly the grasses; however, *Eupatorium maculatum* cover did peak at ~40 % saturation (Figure 5.6b), without a peak in Figure 5.6a. Irrespective of saturation, *Carex stricta* displayed a cover maximum at 38 cm water table amplitude, without predicted cover in areas subject to less than 25 cm seasonal fluctuation. In contrast, *C. livida* cover peaked at just 17 cm amplitude, and was not predicted to grow in sites with more than 25 cm fluctuation (Figure 5.6c). The grasses generally decreased in cover with increasing water table fluctuation, with the exception of *Calamagrostis canadensis*, whereas five of the six shrubs analyzed displayed unimodal sensitivity to water table amplitude.

Sedge species cover proved to be highly sensitive to percent organic matter content in the peat, with unimodal responses to all six analyzed species (Figure 5.7a). While many of the herbs reached maximum cover with lower organic matter (except for *M. trifoliata* and *S. uliginosa*), all grasses reached maximum predicted cover in sites with >50 % organic matter. The three willow species, *Salix candida*, *S. pedicellaris*, and *S. petiolaris* showed vastly different responses, peaking at 70 %, increasing, and decreasing with increasing organic matter content, respectively (Figure 5.7a). Increasing peat calcium carbonate content tended to decrease individual species cover, particularly among the grasses and sedge allies, where predicted cover was zero at > 40 % $CaCO_3$ (Figure 5.7b). *Carex aquatilis* and *Eupatorium maculatum* did, however, actually increase in cover with increasing $CaCO_3$ content.

Only *M. trifoliata* showed a unimodal response to bulk density, peaking at ~0.1 g cm^{-3} (Figure 5.7c). There was a clear separation among the sedges, with *C. lacustris* and *C. flava* increasing with increasing bulk density and the remaining four decreasing. All grasses were subject to reduced covers with increasing bulk density, while the herbs and shrubs displayed varied responses. *Rhamnus alnifolia* was not present in sites with bulk densities lower than 0.14 g cm^{-3}, after which bulk density had no effect on plant species cover (Figure 5.7c).

In general the nutrient gradients proved less useful in eliciting plant species responses (Figure 5.8). Only *Lycopus uniflorus* displayed a unimodal response to dissolved inorganic nitrogen (Figure 5.8a). Most sedges showed a decreased cover response to increased nitrogen presence, while most grasses proved to be invariant to nitrogen levels above 0.5 mg L^{-1}. In contrast, increasing nitrogen availability led to continued increases in *C. stricta* and *Eleocharis erythropoda* cover. Herbaceous species cover, as well as *C. flava*, *C. lacustris*, and *C. lasiocarpa* cover, was drastically reduced when phosphate concentrations reached > 25 mg P L^{-1}, whereas both *Calamagrostis canadensis* and *Typha* spp. increased cover with increasing P-availability (Figure 5.8b). *Carex livida*, *M. trifoliata*, *M. glomerata*, *Rhynchospora fusca*, *Rubus pubescens*, and *S. candida* all displayed local cover maxima around 20-30 mg L^{-1}: these species all co-existed in the northern portion of the Riparian Fen. *Eupatorium maculatum* had a very sharp response to both phosphorus and potassium concentrations (Figure 5.8b-c). In contrast, several other species analyzed showed either no or a very gentle response to increasing potassium concentration. Where a unidirectional response was generated, it was generally a predicted increase in species cover with increasing potassium (Figure 5.8c). *Carex aquatilis*, *M. trifoliata*, *S. uliginosa*, and *Cornus stolonifera* all displayed an elongated unimodal response to the potassium gradient (Figure 5.8c).

Of all the environmental variables tested, the duration of initial saturation and the peat organic matter content proved most prolific in determining individual species ranges or tolerances (Figure 5.9). In addition to capturing a portion of the range of 16 and 18 of the 24 species, respectively, for each variable 10 of those species had their full ranges described. The total duration of saturation/flooding and bulk density proved less useful on the basis of only being able to describe seven and five species ranges, respectively. While describing a portion of the range for 12 species, the DIN gradient was also found to be less useful as most of those ranges were incomplete across one or both tails of the measured nitrogen range (Figure 5.9).

The analysis of species range/tolerance demonstrated the relative breadth of the environmental gradients each species was capable of exploiting. *Carex flava* had a wide tolerance of saturation and water table amplitude and bulk density, in addition to being able to exploit any concentration of calcium carbonate and a wide range of organic matter contents (Figure 5.9). In contrast, *Carex livida* had comparatively narrower or restricted tolerances to the hydrological and peat physical gradients, as well as phosphate concentration (Figure 5.9). *C. livida* was also limited to sites with > 2.5 mg K L^{-1}. Both species are considered fen indicator species and were present in approximately the same number of plots across the sites (~ 40 %), though clearly not always the same plots. *Salix candida* had a much narrower tolerance to early season water table drawdown (short duration of initial saturation) and water table amplitude than *S. pedicellaris*, as well as only able to outcompete for resources at lower phosphate levels (Figure 5.9).

The nine environmental gradients tested were found to produce at least a portion of the natural niche of all 24 species analyzed. The ranges of/tolerances to environmental gradients of several species clearly are more related than others. There was a clear shift in ranges between the drier areas of the fens, where *S. petiolaris*, *R. pubescens*, *R. alnifolia*, *M. arvensis*, *E. maculatum*, and *C. stolonifera* had a high tolerance, and the wetter areas, where *C. aquatilis*, *C. livida*, *M. trifoliata*, *L. thrysiflora*, *E. erythropoda*, and *R. fusca* could tolerate the prolonged flooding (Figure 5.9). Only a few species, *C. flava*, *C. aquatilis*, and *E. maculatum*, and to a lesser extent *L .thyrsiflora*, could tolerate calcium carbonate concentrations above 40 %. There was also a clear separation between species that could tolerate a wide range of organic matter contents (including those that tolerate elevated $CaCO_3$ levels) and those that had much narrower ranges confined to the upper end of the organic matter gradient, including *C. canadensis*, *M. glomerata*, *C. lacustris*, and *R. fusca* (Figure 5.9).

5.5 Discussion

5.5.1 Environmental Control of Plant Species Distribution

In this study we have demonstrated that there exists great variability in plant species distribution (Table 5.1; Figure 5.2) and hydrological and biogeochemical gradients (Figures 5.3-5.5) within individual calcareous fens. This variability is heterogeneous (not a linear directed change in space), and the environmental gradients have varying influences on the response and range of numerous vascular plant species (Figures 5.6-5.9). Many of the tested environmental variables are interrelated and/or representative of other unmeasured factors affecting plant growth. For example, organic matter content is clearly related to bulk density and the hydrological variables (Table 5.2). However, each of these gradients produced distinct plant responses that limited their ranges to varying degrees. Organic matter content was far more useful than bulk density as a key variable controlling species ranges, and this is probably related to organic matter in peat being a large store of organic nutrients (Bedford et al., 1999; Bridgham et al. 1998; Duval et al., in prep; Pérez -Corona et al., 1996), rather than direct control of stored carbon.

It has previously been argued that the duration of initial growing season saturation elicits a stronger control on plant species distribution than the median or mean water table position (Chapter 2). Preliminary assessment of both mean and median water table values on species response did not prove fruitful (data not shown), as similar values were found despite great differences in hydroperiod dynamics (see Chapter 2 for details), resulting in a lack of species response. Thus, Figure 5.6a confirms our earlier suggestion that the length of time fen peat is flooded to start a growing season is an effective control on species growth. In the studied calcareous fens this timing was clearly related to distance from the second-order stream, and resulted in a switch from a sedge and grass community dominated by *C. aquatilis*, *C. flava*, *C. livida*, *M. glomerata*, and *M. trifoliata*, to one of three shrub and herbaceous communities dominated by *R. alnifolia*, *C. stolonifera*, *S. petiolaris*, and *S. uliginosa* in the Riparian Fen, *E. maculatum*, *M. arvensis*, and *C. lacustris* in the Trough Fen, and a mixture of the two in the Basin Fen. Sedge species have very extensive aerenchyma development for the transport of oxygen to their roots (Busch, 2001) and many species perform most of their annual life cycle early in the growing season (Bernard, 1990). Thus, it is probable that prolonged initial saturation promotes sedge species outcompeting more robust shrub species that require greater peat aeration for growth. Conversely, restricted or short initial saturation duration allows other species to grow, exhausting nutrient resources and/or light penetration, preventing sedge growth, even if water levels rise later on in the growing season. Previous research has found water level differences to be the strongest predictor of within-site calcareous fen plant distribution (Hájková et al., 2004; Johnson and Steingraeber, 2003; Nekola, 2004), but to the best of our knowledge, no previous study has directly tested the effect of duration of initial growing season saturation on wetland species distribution, and our data suggest future research in this area is warranted.

The tussock forming sedge *Carex stricta* generally did not follow the patterns observed for the other sedge species. The upper range of this species in response to initial saturation duration and total saturation was not captured in the hydrological regime, similar to the response of the *Typha spp.*, and was the only sedge species tested to increase in cover with increasing DIN content. While not an aquatic plant like *Typha spp.*, tussocks of dead plant material, organic matter, and rhizomes elevated the aboveground portion of *C. stricta* up to 80 cm above the fen peat surface; hence, it is somewhat unsurprising that this species can tolerate even longer durations of saturation than the other sedge species. Additionally, the tussocks formed by *C. stricta* provide refuge for a number of other species above the level of standing water (Peach and Zedler, 2006). Of the 20 quadrats sampled in the Basin Fen seven included portions of or complete *C. stricta* tussocks, and the quadrats in south end of the Trough Fen included three tussocks. These quadrats were associated with local peaks in species richness, diversity, and nutrients.

Compared to the hydrological and peat physical gradients the nutrient gradients were not as useful in producing clear responses to the selected plant species. This was particularly true for DIN; however, DIN concentrations were much higher than phosphorus levels, suggesting that nitrogen is not a limiting nutrient in these settings and would not be expected to limit species ranges (Bedford et al., 1999). On the other hand our results are in line with the majority of other studies that have found very low available phosphorus levels in calcareous fens (Bowles et al., 2005a, 2005b; Boyer and Wheeler, 1989; Johnson and Steingraeber, 2003; Nekola, 2004; Vitt and Chee, 1990). It was somewhat surprising that many of the species responded with decreasing concentrations to increasing P levels or a unimodal response in the lower range of P values (Figure 5.8b). This suggests that calcareous fen plant species not only tolerate low P levels, but also are particularly well adapted to compete for this scarce resource. The potassium levels in the studied calcareous fens were at the high end of fen concentrations reported in the literature (Boyer and Wheeler, 1989; Picking and Veneman, 2004; Verhoeven et al., 1996; Vitt and Chee, 1990), and while few studies have documented or inferred potassium as a limiting nutrient (Olde Venterink et al., 2001; van der Hoek et al., 2004), the results here demonstrate a variable response of some species to these elevated levels. We sampled shallow fen pore-water over two days in early August, after most of the plants had completed the bulk of their growth and seasonal life cycle. It is therefore possible that much of the variability in seasonal nutrient availability was not captured by our sampling strategy. Mean phosphate and nitrate levels were indeed significantly higher throughout the peat profile in August of 2008 compared to other months (Chapter 4). Thus, an earlier sampling date for available nutrients may have yielded tighter nutrient control on plant species distribution.

5.5.2 Calcareous Fen Ecosystem Functioning

This study confirms the notion that calcareous fen species diversity is "greater than the sum of its parts". That is, it is the varied responses of the individual species to the hydrological and biogeochemical gradients that lead to a spatial distribution of differential communities, rather than a single community of large numbers in small proportions across a site. No individual quadrat in the Riparian West, Trough, or Basin Fens had as high diversity as the entire sites (*cf.* Figure 5.2, Table 5.1). While previous vegetation studies of fens have indeed documented within-site species variation (Hájková et al., 2004; Johnson and Steingraeber, 2003; Nekola, 2004) they have been in large peatland systems that encompass a large portion of the poor-rich fen gradient and/or within-site variation was masked by greater between-site variation in the controlling environmental variables. Our results demonstrate that much of the same environmental variability, both hydrologically and geochemically, that leads to high species diversity between fens or across large fen complexes is also present within small calcareous fens. This has important implications for calcareous fen management, as attempts to unify calcareous fen function have been based on limited within-site sampling in favour of characterizing the different settings that lead to calcareous fen formation (Amon et al., 2002; Bedford and Godwin, 2003; Godwin et al., 2002)

The marl flat in the Riparian Fen had the lowest plant species richness and diversity of the calcareous fens, as well as comparatively lower biomass (Duval, unpublished data). A similar finding was documented in calcareous fens of Colorado (Cooper, 1996; Johnson and Steingraeber, 1993) and Illinois USA (Bowles et al., 2005b). However, it is far more common to find marl flats as locations of the greatest richness and diversity (Amon et al., 2002; Boeye and Verheyen, 1994; Boyer and Wheeler, 1989;

Gilvear et al., 1993). In the Western Carpathians of Europe, marl flats are associated with a community shift to more mesotrophic species (Hájková et al., 2004). Thus, it seems the marl flat can occupy varying roles in calcareous fen functioning. We have shown previously that the marl flat in the present study occupies a backwater position from the stream in the Riparian Fen, and is subject to very reduced conditions producing copious toxic hydrogen sulphide gas (Chapter 4). The marl flat in the calcareous fen studied by Bowles et al. (2005b) was also situated a great distance from the groundwater seeps, though no information on redox species was provided. Marl flats or tufa mounds that host high plant species richness and diversity typically are sites of groundwater discharge (Boyer and Wheeler, 1989), where the continual supply of electron acceptors prevents severe reducing conditions (Almendinger and Leete, 1998a; Lucassen et al., 2004). The Western Carpathian marl flats are sites of greater water table drawdown than the surrounding areas (Hájková et al., 2004). Based on this, we suggest a conceptual model of calcareous fen ecosystem functioning must account for the varying within-fen landscape positions of marl flats, as these areas can have contrasting roles in fen vegetation dynamics. More research is required on the variability in marl flats in calcareous fens to fully develop this conceptual model.

5.5.3 Use of Non-Linear Quantile Regression

In this study we show the usefulness of fitting the 95th quantile of a species response to individual environmental gradients in calcareous fens, where individual species rarely make-up a majority of areal cover. Previously, Schröder et al. (2005) demonstrated the usefulness in fen ecosystems characterized by monotypic stands along environmental gradients. Thus, this method of analysis, when combined with the asymmetric logistic response function proposed by Huisman et al. (1993), is capable of identifying individual species niches across numerous hydrological and biogeochemical gradients in fen systems where species cover ranges from 100 % to as little as 3 % (*Eleocharis erythropoda* in response to duration of initial saturation, Figure 5.6a). This method does not group species into assemblages as in two-way indicator species analysis or against a group of environmental gradients. As such, it can be construed as less robust than those techniques for its inability to define communities. However, non-linear quantile regression is a very powerful tool for determining the true range of a species in response to a single environmental gradient (Austin, 2007), which is commonly less than its potential range due to competition and limitations of other environmental gradients (Schröder et al., 2005). Therefore, in its strictest sense, this method of analysis is capable of determining an individual species realized niche. Cumulatively then, this approach does predict species assemblages based on individual responses to measurable environmental gradients.

5.5.4 Implications for Conservation

One promising avenue of use for the data generated here, and non-limiting quantile regression in general, is in the conservation, restoration, and creation of ecosystems. We have generated a dataset of species responses and ranges to a suite of hydrological and biogeochemical gradients present within three calcareous fens of a larger wetland complex. Several studies have investigated the degradation of fens both in terms of physical, hydrological, and biogeochemical alteration, and loss of characteristic and/or rare vascular plant species (Aldous et al., 2005; Beumer et al., 2008; Billeter et al., 2003; Boeye et al., 1995; Bowles et al., 2005a; Cooper and MacDonald, 2000; Geurts et al., 2009; Grootjans et al., 2006; Jansen et al., 2001; Kooijman and Hedenäs, 2009; Lamers et al., 2002). Our data, and similarly generated datasets, can serve as assessment tools for the degree of fen ecosystem impact and/or predictors of successful restoration measures. Additionally, recent attempts at calcareous wetland creation (Amon et al., 2005; Duval et al., 2010) can be aided by specific knowledge of suitable species for transplant/planting given *in situ* hydrological regimes and physiochemical environments.

5.6 Conclusion

The controls of hydrological and biogeochemical variables on plant species dynamics within calcareous fens were tested. Plant species richness and diversity was variable across the fens, with contiguous fen species diversity being greater than finer-scale measurements in all cases, confirming that the high species diversity of calcareous fens is the result of within-site environmental gradients, and not the result of a heterogeneous but unchanging community across a site. Non-linear quantile regression was used to link plant species distribution to measured hydrological and biogeochemical gradients within three calcareous fens. Species responses were varied, ranging from linear, curvilinear, and monotonic changes to symmetric and asymmetric logistic in shape. The duration of initial growing season saturation and the organic matter content of the surface peat were most useful in generating meaningful responses to the species tested, while bulk density and dissolved inorganic nitrogen content were less useful. This dataset can be used by fen restoration and creation projects to aid the decision making process. Our data suggest refinement of the conceptual model of calcareous fen ecosystem functioning is needed to address plant physiological responses to the varied interaction of hydrological flowpaths and biogeochemical reactions that can occur within and between calcareous fens.

5.7 Acknowledgements

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Table 5.1: Calcareous fen vascular plant species biodiversity summaries.

	Area (ha)	Species Richness	Species Diversity	Sørensen's Coefficient of Similarity			
				RW	RE	TF	BF
Riparian West	1.7	63	3.06	X			
Riparian East	3.0	45	1.89	0.50	X		
Trough Fen	2.2	64	2.71	0.40	0.42	X	
Basin Fen	0.45	41	2.43	0.43	0.45	0.57	X

Table 5.2: Correlation coefficients of environmental variables and species richness and diversity in the studied calcareous fens.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1: Peat Depth	X														
2: Moisture	0.64^{***}	X													
3: pH	~	~	X												
4: EC	0.53^{***}	~	~	X											
5: Bulk Density	-0.27^{**}	-0.66^{***}	~	~	X										
6: Organic Matter	~	0.69^{***}	-0.55^{***}	-0.50^{***}	-0.59^{***}	X									
7: $CaCO_3$	~	-0.50^{***}	0.29^{**}	0.51^{***}	0.45^{***}	-0.85^{***}	X								
8: Initial Saturation	0.23^{*}	~	0.56^{***}	0.27^{*}	~	-0.30^{**}	~	X							
9: Total Saturation	~	0.22^{*}	0.60^{***}	~	-0.25^{**}	~	~	0.77^{***}	X						
10: WT Amplitude	-0.81^{***}	-0.73^{***}	~	-0.48^{***}	0.40^{***}	-0.22^{*}	~	-0.52^{***}	-0.41^{***}	X					
11: DIN	~	~	~	-0.23^{*}	~	~	~	~	~	~	X				
12: P	0.23^{*}	0.25^{**}	~	-0.28^{*}	-0.33^{***}	0.43^{***}	-0.26^{**}	~	~	~	0.46^{***}	X			
13: K	0.75^{***}	0.51^{***}	-0.23^{*}	0.46^{***}	-0.21^{*}	0.21^{*}	~	~	~	-0.60^{***}	~	0.21^{*}	X		
14: Richness	~	~	~	~	~	0.24^{**}	-0.31^{***}	~	-0.26^{**}	~	~	~	~	X	
15: Diversity	~	~	~	-0.28^{*}	~	0.29^{**}	-0.36^{***}	~	~	~	~	~	~	0.84^{***}	X

$* = P < 0.05$; $** = P < 0.01$; $*** = P < 0.001$; ~ = non-significant correlation.

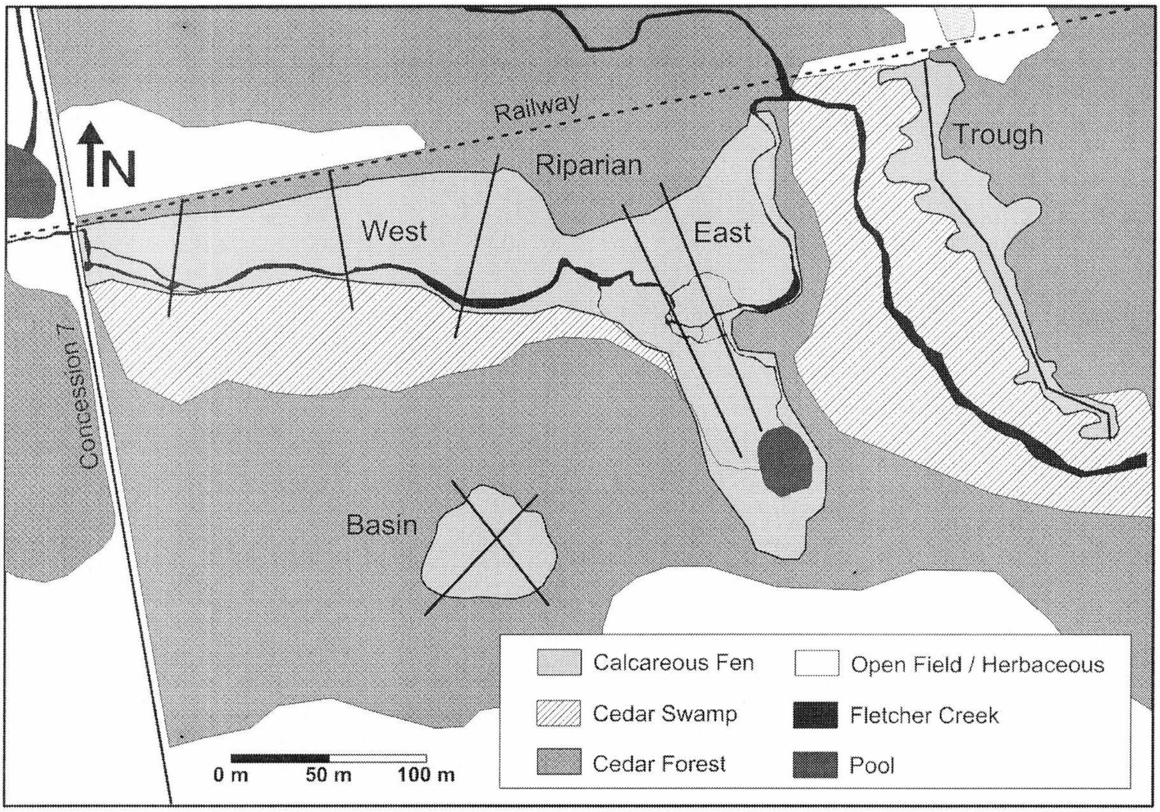

Figure 5.1: Study site map, indicating position of calcareous fens. Solid straight black lines indicate location of vegetation sampling quadrats.

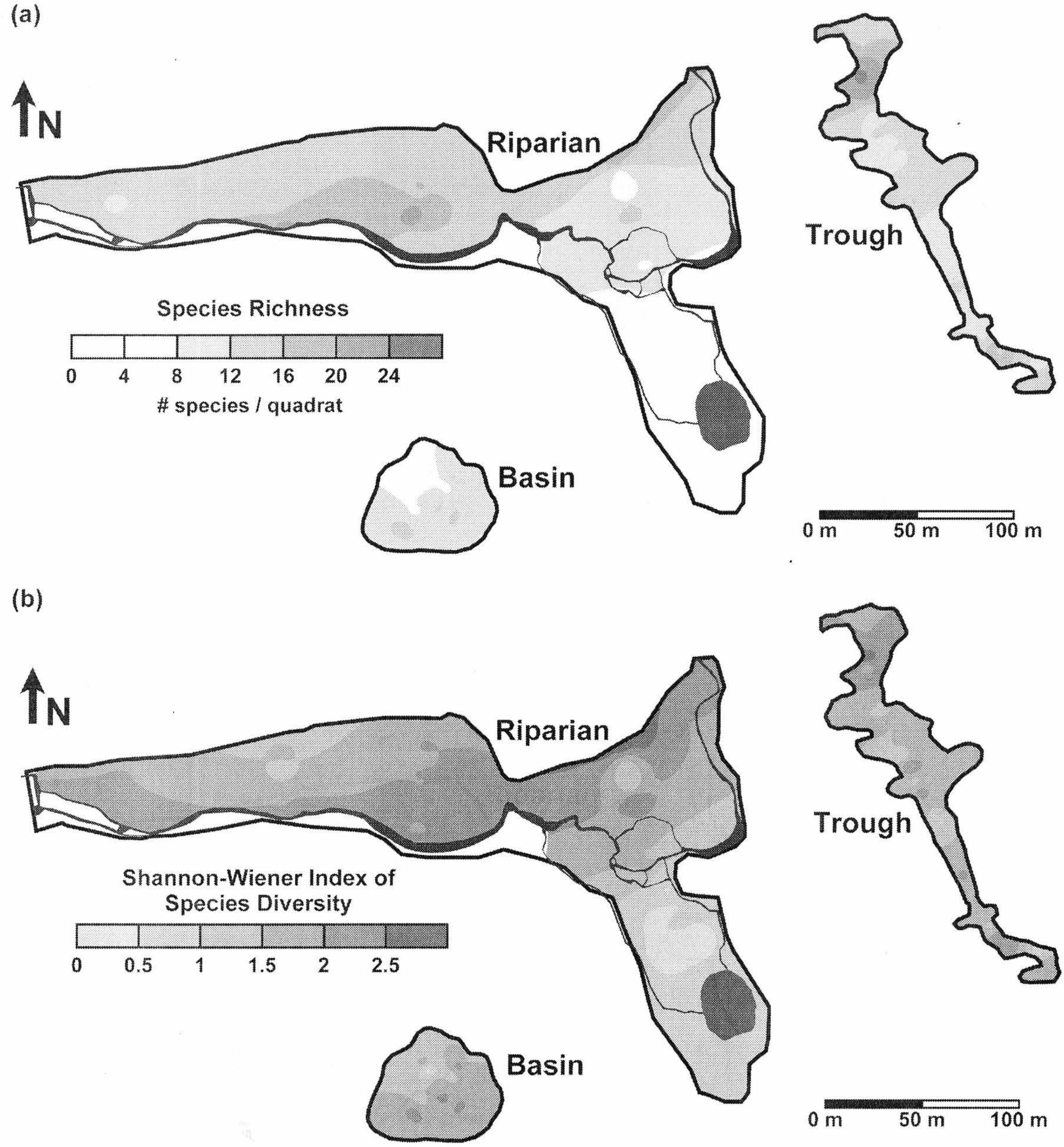

Figure 5.2: Spatial distribution of (a) species richness and (b) species diversity in the calcareous fens.

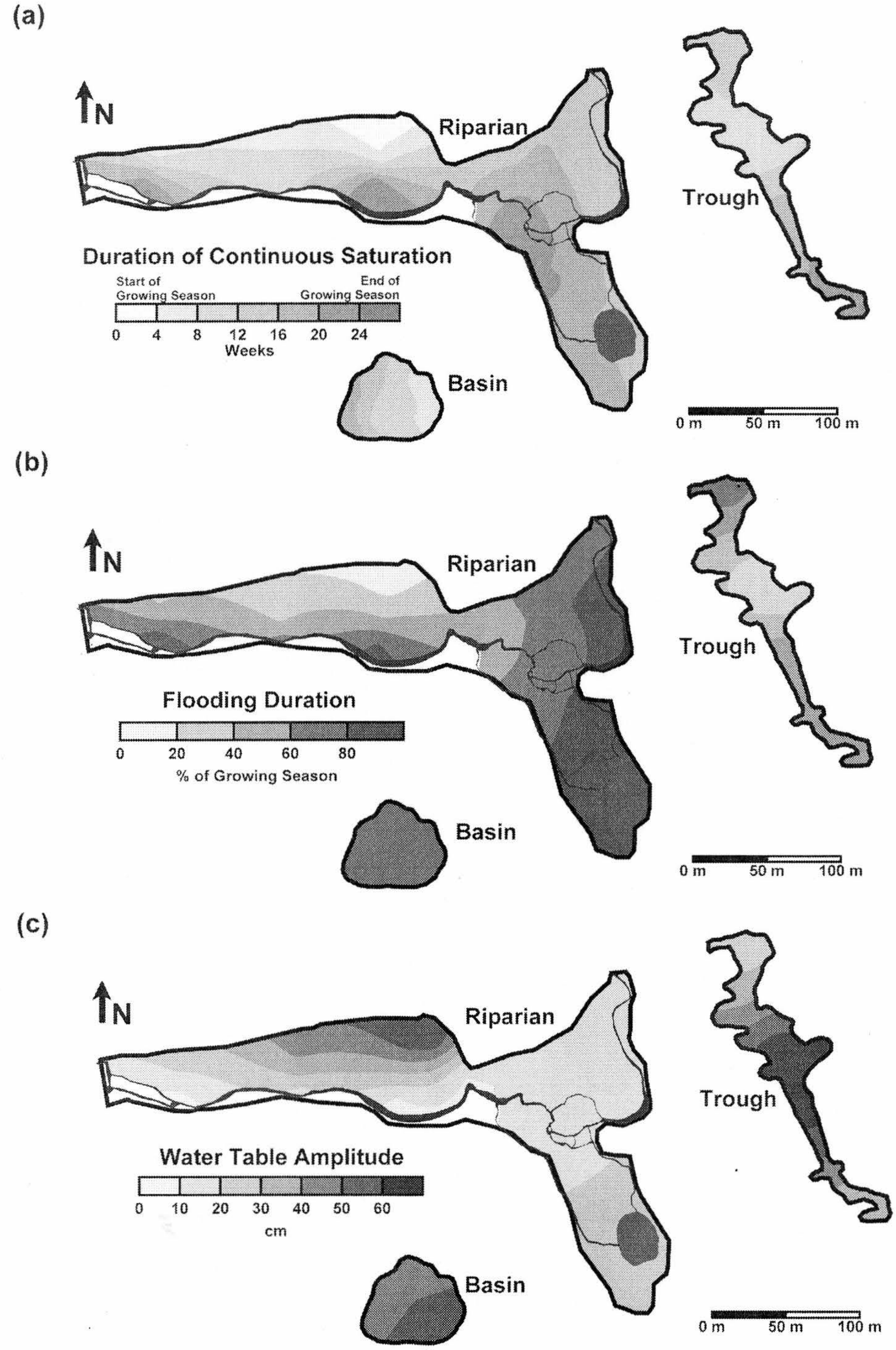

Figure 5.3: Hydrological gradients in the calcareous fens: (a) duration of initial saturation from start of growing season; (b) percentage of growing season saturation; (c) water table amplitude throughout the growing season.

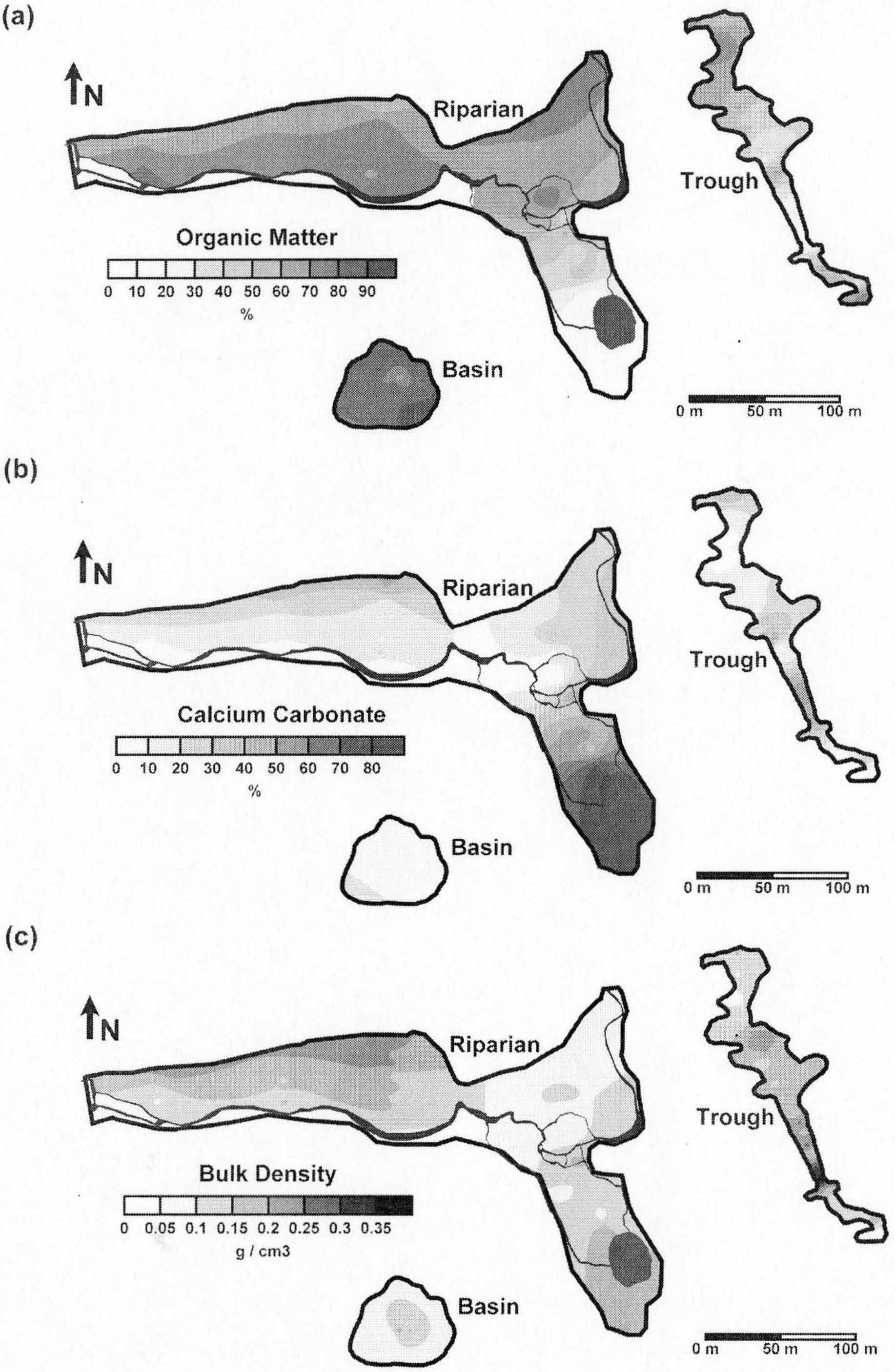

Figure 5.4: Physical gradients of the upper 20 cm of peat in the calcareous fens: (a) organic matter content; (b) calcium carbonate (equivalent) content; (c) bulk density.

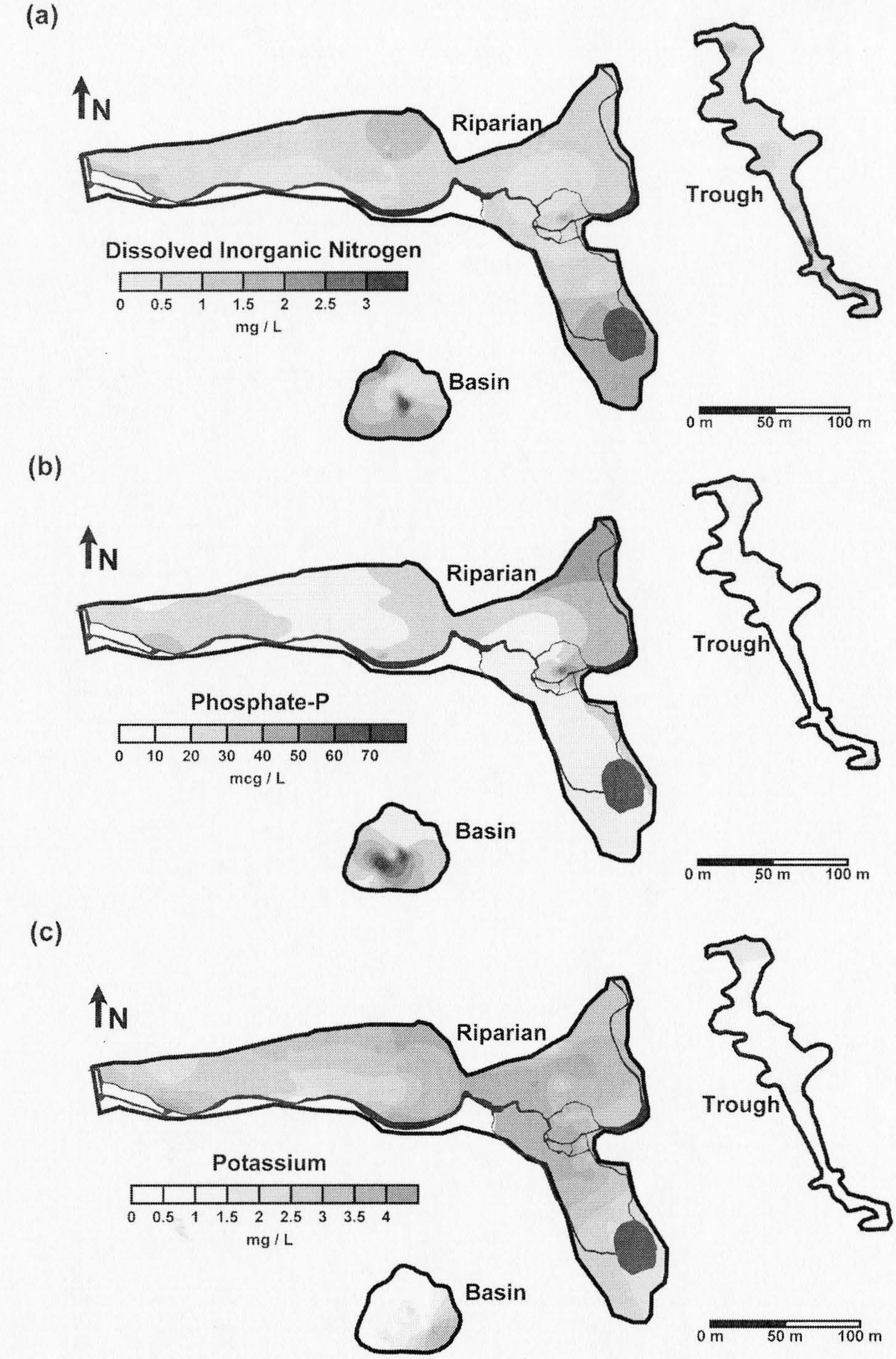

Figure 5.5: Nutrient gradients in the shallow peat pore-water in the calcareous fens: (a) total dissolved inorganic nitrogen (NO_3^--N + NH_4^+-N); (b) phosphorus (PO_4^{3-}-P); (c) potassium.

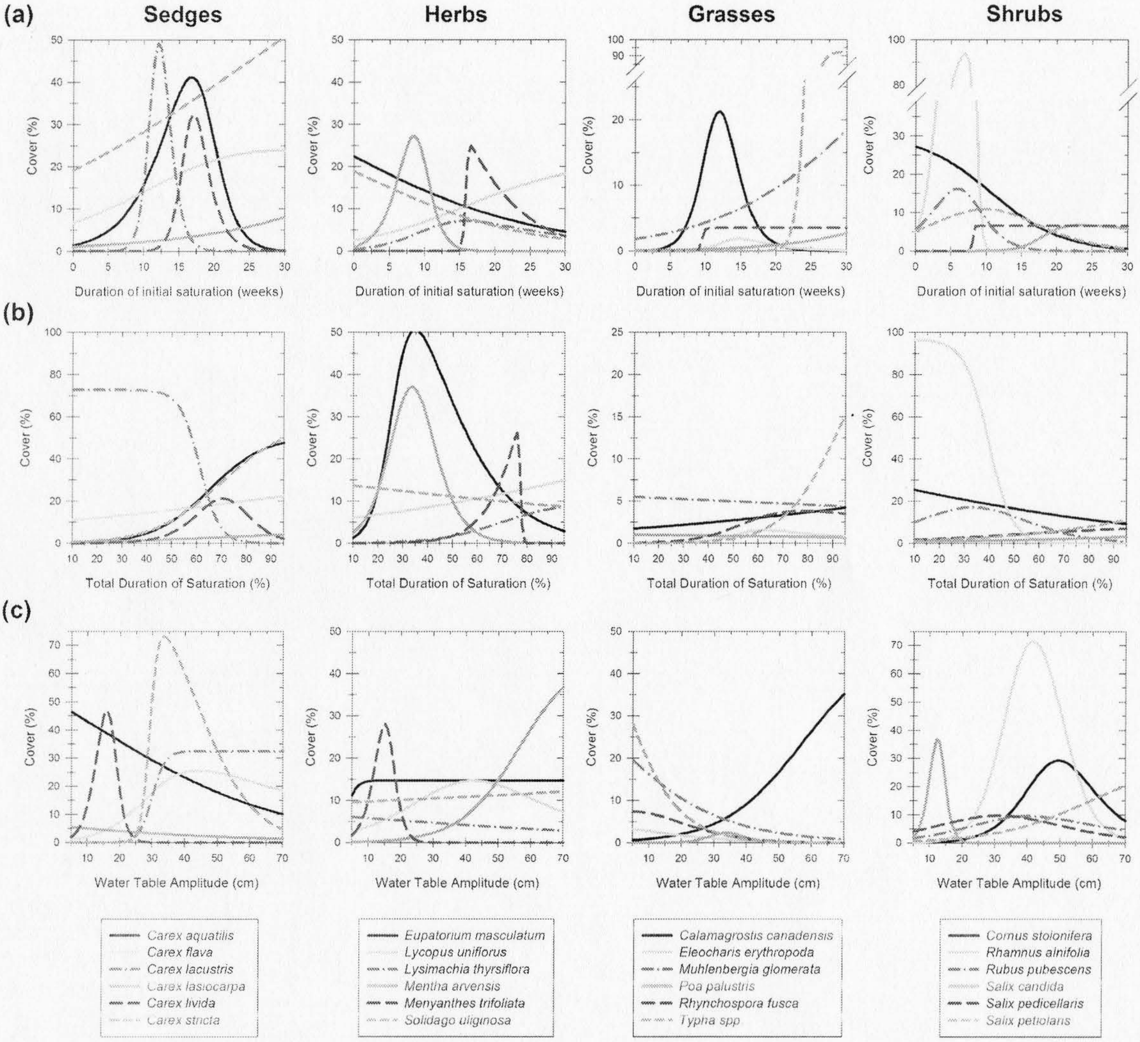

Figure 5.6: Species response to hydrological gradients: (a) duration of initial saturation; (b) total duration of saturation; (c) water table amplitude. The graphs depict the response function of the 95th % quantile of measured species cover. Species are grouped according to growth form: true sedges (*Carex* species); herbaceous species; grasses and sedge-allies and aquatics; and, shrubs.

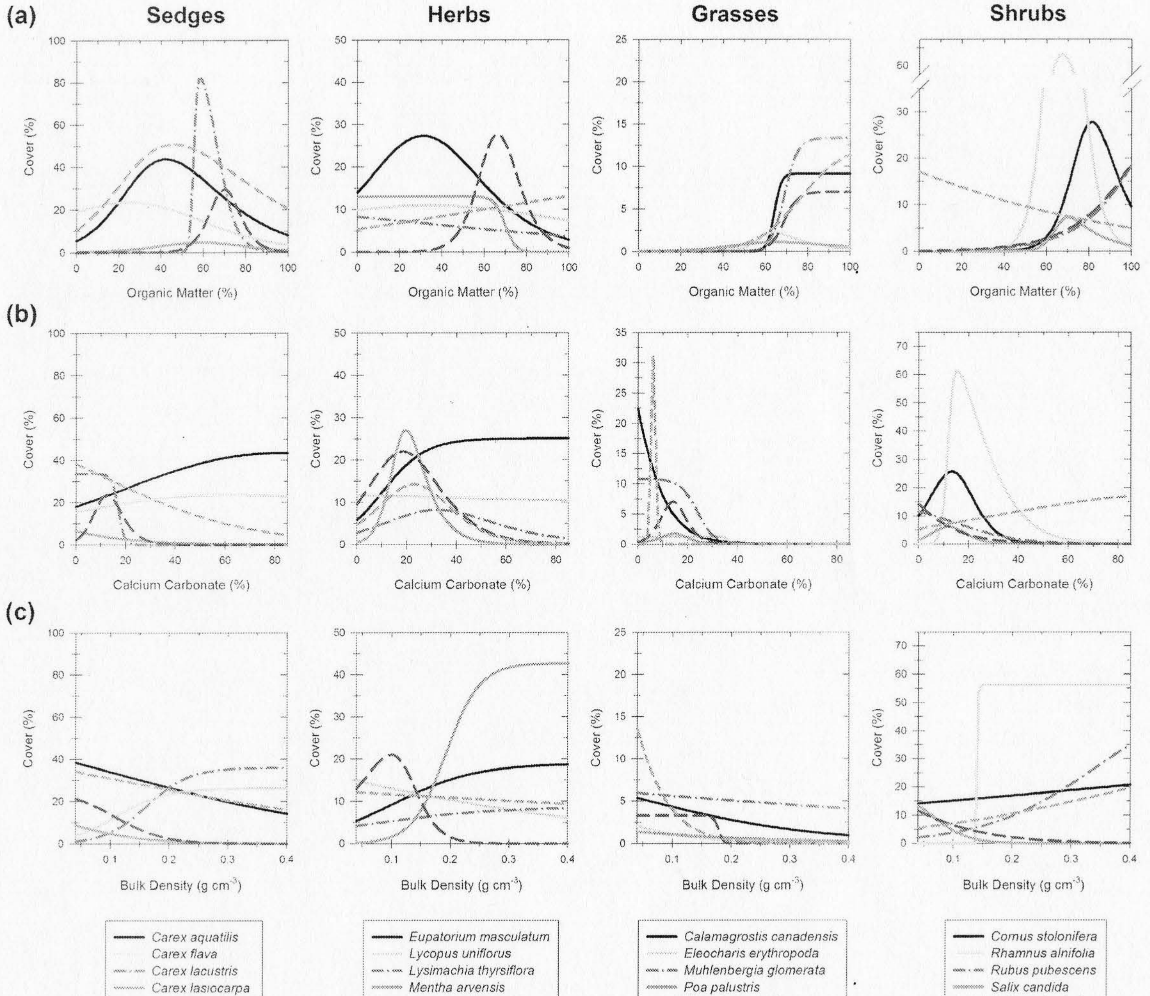

Figure 5.7: Species response to peat physical gradients: (a) organic matter; (b) calcium carbonate content; (c) bulk density. The graphs depict the response function of the 95th % quantile of measured species cover. Species are grouped according to growth form: true sedges (*Carex* species); herbaceous species; grasses and sedge-allies and aquatics; and, shrubs.

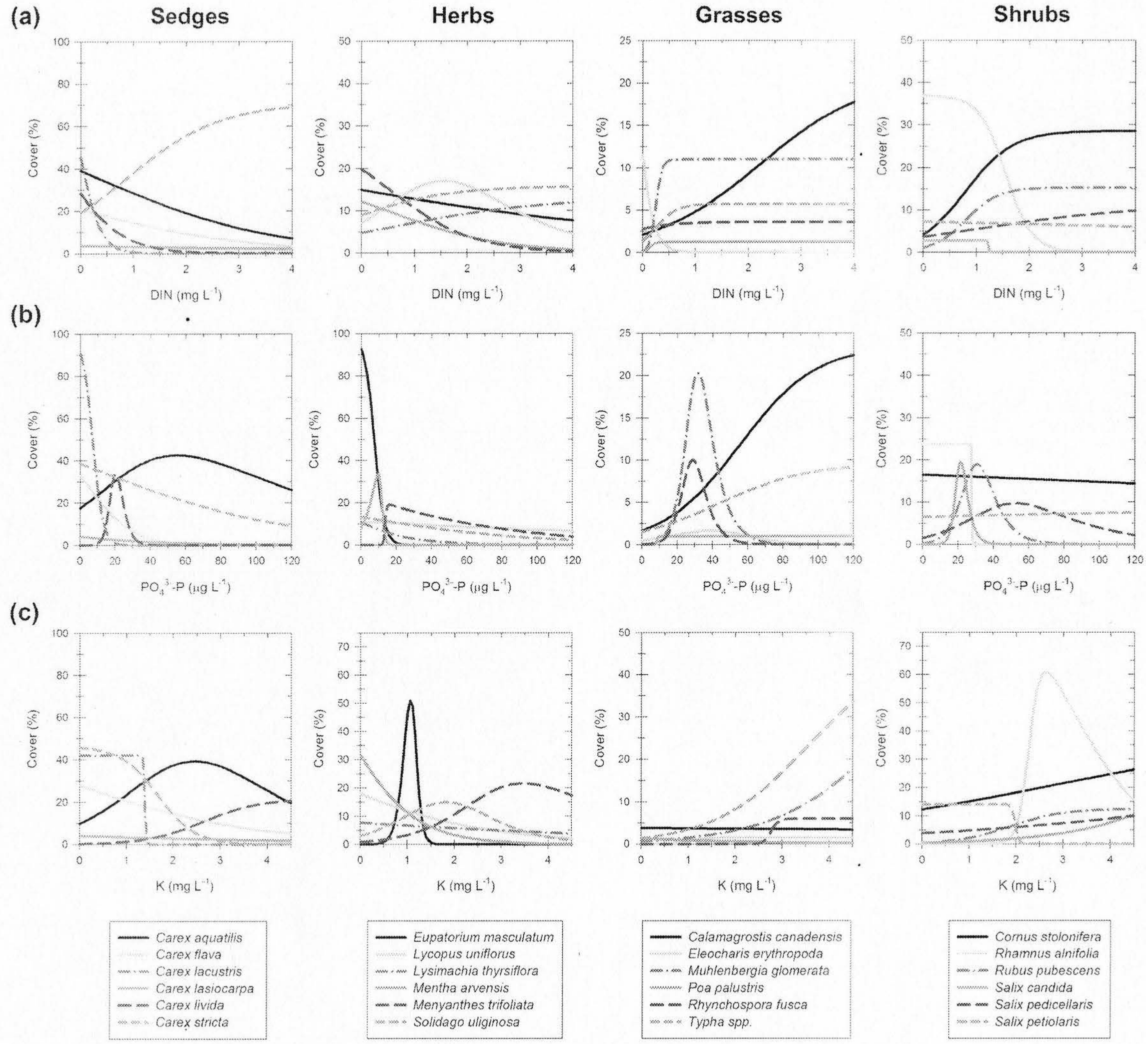

Figure 5.8: Species response to pore-water nutrient gradients: (a) dissolved inorganic nitrogen; (b) phosphate-P; (c) potassium. The graphs depict the response function of the 95th % quantile of measured species cover. Species are grouped according to growth form: true sedges (*Carex* species); herbaceous species; grasses and sedge-allies and aquatics; and, shrubs.

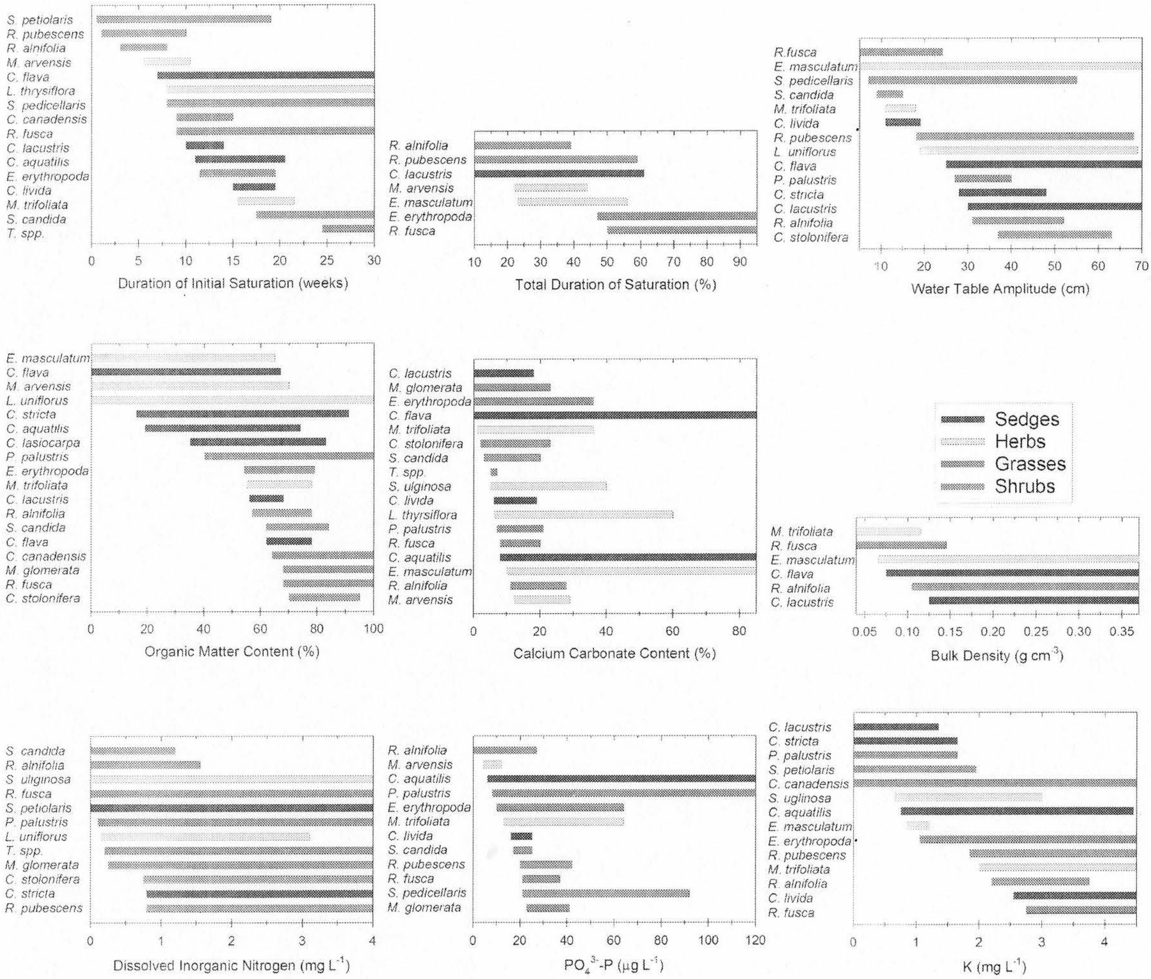

Figure 5.9: Species ranges/tolerances to the measured environmental variables. For each species, bar width represents that part of the environmental gradient where cover was greater than 50 % of the maximum predicted cover. Species not present in a graph indicate the respective measured environmental variable range did not produce a sufficient response in plant cover to estimate a range.

5.9 Appendix 5.1

Species Present in the Studied Calcareous Fens, Grouped by Growth Type and Site.

Presence is further sub-divided by percentage areal coverage: - = no presence, + = < 1 % at a site, other classes as %.

	Latin Name	Common Name	Riparian West	Riparian East	Trough	Basin
Sedges						
	Carex aquatilis	Water Sedge	+	5 - 25	5 - 25	1 - 5
	Carex bebbii	Bebb's Sedge	-	-	+	-
	Carex cryptolepis	Hidden Scale Sedge	+	-	-	-
	Carex diandra	Lesser Panicled Sedge	-	+	+	-
	Carex flava	Yellow Sedge	1 - 5	+	5 - 25	-
	Carex hirta	Hammer Sedge	-	-	+	-
	Carex hystericina	Porcupine Sedge	-	+	-	+
	Carex interior	Inland Sedge	+	-	+	-
	Carex lacustris	Lakebank Sedge	-	-	5 - 25	+
	Carex lasiocarpa	Wire Sedge	+	+	1 - 5	+
	Carex limosa	Candle Lantern Sedge	-	+	-	-
	Carex livida	Livid Sedge	1 - 5	5 - 25	+	+
	Carex lupuliformis	False-Hop Sedge	-	-	1 - 5	-
	Carex michauxiana	Michaux's Sedge	-	-	+	-
	Carex prairea	Prairie Sedge	+	1 - 5	+	-
	Carex stricta	Tussock Sedge	-	-	5 - 25	5 - 25
	Carex utriculata	Beaked Sedge	-	-	-	5 - 25
	Carex vesicaria	Inflated Sedge	-	-	1 - 5	-
	Carex viridula	Green Sedge	+	-	-	-
	Dulichium arundinaceum	Three-way Sedge	-	-	-	1 - 5

Latin Name	Common Name	Riparian West	Riparian East	Trou ı	Basin
Sedges concluded					
Eleocharis compressa	Compressed Spikerush	+	-	-	-
Eleocharis erythropoda	Red-stemmed Spikerush	+	+	+	+
Eleocharis smallii	Marsh Spikerush	+	+	+	-
Rhynchospora alba	White Beakrush	+	-	+	-
Rhynchospora fusca	Brown Beakrush	+	-	+	-
Scirpus acutus	Hard-stemmed Bul Rush	-	1 - 5	-	-
Scirpus cespitous	Tufted Clubrush	-	-	+	-
Scirpus hudsonianus	Hudson Bay Clubrush	+	-	-	-
Scirpus validus	Soft-stemmed Bul Rush	-	-	-	+
Grasses and Rushes					
Calamagrostis canadensis	Canada Blue Joint	+	+	1 -	1 - 5
Cinna latifolia	Drooping Woodreed	+	-	+	-
Glyceria striata	Fowl Manna Grass	-	-	+	-
Juncus Canadensis	Canada Rush	-	-	+	-
Muhlenbergia glomerata	Marsh Timothy	1 - 5	+	+	+
Phalaris arundinacea	Reed Canary Grass	-	-	+	-
Phragmites australis	Commone Reed Grass	+	-	+	-
Poa palustris L.	Fowl Meadow Grass	+	-	+	+
Herbs and Forbs					
Asclepias incarnata	Marsh Milkweed	-	-	+	-
Bidens cernua	Nodding Beggartick	-	+	-	-
Bidens connata	Northern Burr Marigold	-	-	+	-
Caltha palustris	Marsh Marigold	+	+	-	-
Campanula aparinoides	Marsh Bellflower	+	-	+	-

Latin Name	Common Name	Riparian West	Riparian East	Trough	Basin
Herbs and Forbs continued					
Chelone glabra	Turtlehead	-	-	+	1 - 5
Cicuta bulbifera	Bulbiferous Water Hemlock	-	+	+	+
Cypripedium reginae	Showy Lady's Slipper	1 - 5	-	-	-
Epilobium palustre	Marsh Willowherb	+	+	+	-
Erigeron philadelphicus	Philadelphia Fleabane	-	-	+	-
Eupatorium maculatum	Spotted Joe-Pye weed	+	-	5 - 25	1 - 5
Eupatorium perfoliatum	Boneset	-	-	1 - 5	+
Eupatorium rugosum	Eupatorium rugosum	-	-	+	+
Galium labradoricum	Labrador Bedstraw	+	+	+	+
Galium trifidum	Small Bedstraw	+	+	+	1 - 5
Galium triflorum	Fragrant Bedstraw	-	+	-	-
Impatiens capensis	Spotted Touch-me-not	-	+	1 - 5	-
Iris versicolor	Northern Blue Flag	+	+	-	1 - 5
Liparis loeselii	Fen Twayblade	+	+	-	+
Lycopus americanus	Water Horehound	+	-	+	+
Lycopus uniflorus	Northern Bugleweed	1 - 5	+	1 - 5	1 - 5
Lysimachia thyrsiflora	Tufted Loosetrife	+	1 - 5	1 - 5	1 - 5
Lythrum salicaria	Purple Loosestrife	+	+	-	-
Mentha arvensis	Wild Mint	-	-	1 - 5	-
Menyanthes trifoliata	Bogbean	1 - 5	5 - 25	-	-
Nasturtium officinale	Watercress	+	1 - 5	+	+
Polygonum amphibium	Water Smartweed	-	-	-	1 - 5
Sarracenia purpurea	Pitcher Plant	1 - 5	-	-	-
Solanum dulcamara	Creeping Nightshade	-	+	+	+

Latin Name	Common Name	Riparian West	Riparian East	Trough	Basin
Herbs and Forbs concluded					
Solidago graminifolia	Grass-leaved Goldenrod	+	-	+	-
Solidago rugosa spp. rugosa	Rough-stemmed Goldenrod	+	-	+	+
Solidago uliginosa	Bog Goldenrod	1 - 5	+	1 - 5	1 - 5
Scutellaria galericulata	Skullcap	-	+	+	+
Symphyotrichum lanceolatum	Lance-leaved Aster	-	-	1 - 5	+
Symphyotrichum novae-angliae	New England Aster	-	-	+	-
Symphyotrichum puniceum	Purple-stemmed Aster	-	+	-	-
Symphyotrichum boreale	Rush Aster	1 - 5	-	+	+
Triadenum fraseri	Marsh St John's-Wort	-	-	+	-
Viola nephrophylla	Northern Bog Violet	1 - 5	+	-	-
Viola palustris	Northern Marsh Violet	+	+	-	-
Viola spp.	Violet Spp.	1 - 5	+	1 - 5	-
Shrubs, Trees, Ferns, and Aquatics					
Andromeda glaucophylla	Bog Rosemary				
Alnus rugosa	Speckled Alder	+	+	-	-
Chara spp.	Stonewort	-	1 - 5	-	-
Equisetum fluviatile	Water Horsetail	+	-	-	-
Equisetum palustre	Marsh Horsetail	+	-	1 - 5	-
Cornus alternifolia	Alternate-leaved Dogwood	+	-	-	-
Cornus stolonifera	Red Oisier Dogwood	1 - 5	-	+	1 - 5
Kalmia angustifolia	Sheep Laurel	+	-	-	-
Larix laricina	Tamarack	1 - 5	+	+	+
Ledum groenlandicum	Labrador Tea	1 - 5	-	-	-

Latin Name	Common Name	Riparian West	Riparian East	Trough	Basin
Shrubs, Trees, Ferns, and Aquatics concluded					
Lonicera villosa	Mountain Fly Honeysuckle	+	-	-	-
Myrica gale	Sweet Gale	-	-	+	-
Onoclea sensibilis	Sensitive Fern	-	-	+	-
Rhamnus alnifolia	Alder-leaved Buckthorn	5 - 25	-	-	-
Rhamnus frangula	Glossy Buckthorn	1 - 5	-	-	-
Rubus pubescens	Dwarf Raspberry	1 - 5	+	-	1 - 5
Salix bebbiana	Bebb's Willow	+	-	-	-
Salix candida	Sage Willow	+	1 - 5	-	-
Salix pedicellaris	Bog Willow	+	1 - 5	-	1 - 5
Salix petiolaris	Slender willow	+	+	1 - 5	1 - 5
Thelypteris palustris	Marsh Fern	5 - 25	+	+	1 - 5
Thuja occidentalis	Eastern White Cedar	1 - 5	-	1 - 5	+
Typha spp.	Cattail spp.	1 - 5	+	+	+
Vaccinium myrtilloides	Velvet-leaved Blueberry	+	+	-	-
Vaccinium oxyoccos	Small Cranberry	+	-	-	-

App. 5.1 Continued. Parameters of Fitted Cover Response Functions for the Selected Species and Environmental Gradients.

Duration of Initial Saturation (weeks)				
Species	a	b	c	d
Carex aquatilis	4.284045	-0.261366	-10.9471	0.575507
Carex flava	1.822919	-0.118146	0.081870	0.028735
Carex lacustris	14.29863	-1.27044	-11.5668	0.900285
Carex lasiocarpa	3.887477	-0.071817	-0.135223	0.000000
Carex livida	-9.77242	0.582777	17.93689	-1.10410
Carex stricta	1.252987	-0.053339	-1.86733	0.000000
Eupatorium maculatum	0.334226	0.068110	-0.152927	0.000000
Lycopus uniflorus	1.992145	-0.124636	1.295349	0.000000
Lysimachia thyrsiflora	3.700715	-0.332356	1.346454	0.064492
Mentha arvensis	-7.65398	0.833839	4.626609	-0.510624
Menyanthes trifoliata	91.83402	-5.81303	-1.68695	0.167327
Solidago uliginosa	-0.067667	0.085467	0.555022	0.000000
Calamagrostis canadensis	-5.25242	0.486175	8.290972	-0.722435
Eleocharis erythropoda	0.628570	0.206308	10.39555	-0.777611
Muhlenbergia glomerata	3.215885	-0.093464	0.140929	0.000000
Poa palustris	6.782945	-0.114560	-1.41429	0.000000
Rhynchospora fusca	48.76243	-5.13312	3.317053	0.000000
Typha spp.	32.87057	-1.33106	-2.50576	0.000000
Cornus stolonifera	-2.15115	0.200800	0.830700	0.000000
Rhamnus alnifolia	2.913087	-0.847491	-24.0288	2.850630
Rubus pubescens	-3.25223	0.510044	2.785731	-0.320376
Salix candida	1.899838	0.028847	11.00100	-0.602061
Salix pedicellaris	92.17483	-11.3691	2.651434	0.000000
Salix petiolaris	-2.26783	0.234234	2.768900	-0.154138

App. 5.1. cont.

Flooding Duration (% of growing season)

Species	a	b	c	d
Carex aquatilis	5.842690	-0.089673	-0.040626	0.000000
Carex flava	1.357956	-0.012792	0.066632	0.000000
Carex lacustris	-15.1597	0.247465	-0.981990	0.000000
Carex lasiocarpa	2.509097	-0.036695	2.788414	0.000000
Carex livida	-11.3791	0.158667	8.844029	-0.119026
Carex stricta	5.145842	-0.073758	-0.297970	0.000000
Eupatorium maculatum	-2.42695	0.062479	6.689563	-0.254248
Lycopus uniflorus	1.908667	-0.013979	0.341141	0.000000
Lysimachia thyrsiflora	5.472976	-0.078602	2.206870	0.000000
Mentha arvensis	-5.30241	0.149304	5.384416	-0.178468
Menyanthes trifoliata	9.801607	-0.116144	-188.289	2.437453
Solidago uliginosa	1.096419	0.006767	-0.315848	0.000000
Calamagrostis canadensis	1.885538	0.000933	2.025172	-0.014618
Eleocharis erythropoda	9.603953	-0.184514	2.552033	0.023448
Muhlenbergia glomerata	2.376527	0.002969	-0.701960	0.000000
Poa palustris	4.245694	0.004617	-1.28167	0.000000
Rhynchospora fusca	2.323153	0.010289	6.012825	-0.106551
Typha spp.	8.373811	-0.090362	0.966897	0.000000
Cornus stolonifera	0.258784	0.015926	-0.584231	0.000000
Rhamnus alnifolia	-8.28381	0.209272	-3.35483	0.000000
Rubus pubescens	2.559223	-0.063276	-2.06831	0.069462
Salix candida	4.412394	-0.016672	-0.395408	0.000000
Salix pedicellaris	1.646193	-0.032899	2.358377	0.000000
Salix petiolaris	3.888514	-0.026691	-0.181070	0.000000

App. 5.1. cont.

Water Table Amplitude (cm)				
Species	a	b	c	d
Carex aquatilis	-0.432077	0.034195	-1.53171	0.000000
Carex flava	4.504439	-0.150069	-0.081056	0.022356
Carex lacustris	15.35493	-0.511829	0.730887	0.000000
Carex lasiocarpa	2.159700	0.023229	-0.417783	0.000000
Carex livida	5.981041	-0.409073	-10.6811	0.602517
Carex stricta	-4.92235	0.113119	23.64340	-0.808019
Eupatorium maculatum	2.108207	-0.650984	1.754397	0.000000
Lycopus uniflorus	-0.819104	0.047470	3.643369	-0.098713
Lysimachia thyrsiflora	1.108043	-0.008826	1.055051	0.020817
Mentha arvensis	6.193576	-0.109665	0.187328	0.000000
Menyanthes trifoliata	5.927205	-0.377791	-9.26256	0.577205
Solidago uliginosa	1.298540	-0.004824	0.252646	0.000000
Calamagrostis canadensis	4.755854	-0.083185	0.103807	0.000000
Eleocharis erythropoda	0.817520	0.090084	1.946736	-0.044251
Muhlenbergia glomerata	0.480134	0.055030	-0.471824	0.000000
Poa palustris	13.72729	-0.387708	-6.12610	0.258831
Rhynchospora fusca	2.080605	-0.074452	-0.517714	0.119761
Typha spp.	0.207482	0.109630	-2.05155	0.000000
Cornus stolonifera	7.616896	-0.164600	-5.41126	0.112168
Rhamnus alnifolia	7.590661	-0.225023	-9.96697	0.200486
Rubus pubescens	0.167040	0.040730	3.635283	-0.108842
Salix candida	-9.39952	0.707369	6.615992	-0.556491
Salix pedicellaris	-1.13336	0.070732	3.164398	-0.085987
Salix petiolaris	4.125327	-0.069324	0.842053	0.000000

App. 5.1. cont.

Organic Matter Content (%)

Species	a	b	c	d
Carex aquatilis	-2.18580	0.046052	2.735587	-0.095340
Carex flava	-1.70378	0.048801	1.233197	-0.030420
Carex lacustris	63.41624	-1.14298	-14.3522	0.215788
Carex lasiocarpa	5.928626	-0.097909	-1.27104	0.058198
Carex livida	-13.9505	0.197305	14.50864	-0.210391
Carex stricta	-1.96190	0.033085	2.002131	-0.078827
Eupatorium maculatum	1.580342	-0.059207	-1.49505	0.050115
Lycopus uniflorus	0.641129	0.016798	0.918785	-0.024457
Lysimachia thyrsiflora	0.744787	0.015199	1.059916	-0.006158
Mentha arvensis	-28.4447	0.407959	1.899313	0.000000
Menyanthes trifoliata	-8.68408	0.133507	11.52300	-0.180273
Solidago uliginosa	0.934596	-0.016761	1.429557	0.000000
Calamagrostis canadensis	39.42693	-0.614597	2.297779	0.000000
Eleocharis erythropoda	-0.415720	0.061544	15.44407	-0.259661
Muhlenbergia glomerata	21.92357	-0.317772	1.872676	0.000000
Poa palustris	2.145010	0.030372	5.543682	-0.096879
Rhynchospora fusca	21.22691	-0.308752	2.592118	0.000000
Typha spp.	7.393983	-0.096395	1.937808	0.000000
Cornus stolonifera	14.79186	-0.191952	-7.53093	0.097572
Rhamnus alnifolia	-14.0789	0.189190	14.68058	-0.242312
Rubus pubescens	6.909316	-0.060384	-0.526159	0.000000
Salix candida	22.13154	-0.335264	-2.60128	0.069903
Salix pedicellaris	6.382711	-0.056681	-0.296271	0.000000
Salix petiolaris	0.921143	0.014689	-0.405912	0.000000

App. 5.1. cont.

Calcium Carbonate Content (%) Species	a	b	c	d
Carex aquatilis	1.171974	-0.032351	-1.19164	0.012942
Carex flava	0.258512	0.009391	0.589346	-0.030661
Carex lacustris	-13.8170	0.811271	0.677696	0.000000
Carex lasiocarpa	1.768259	0.050171	0.158231	0.000000
Carex livida	3.571296	-0.314930	-2.23499	0.209566
Carex stricta	-0.422656	0.034875	-0.547023	0.000000
Eupatorium maculatum	1.191126	-0.116099	1.094609	0.000000
Lycopus uniflorus	0.597580	0.002192	0.708663	0.000000
Lysimachia thyrsiflora	2.680133	-0.089273	0.210075	0.047330
Mentha arvensis	-2.26761	0.141407	5.172267	-0.311393
Menyanthes trifoliata	-1.31818	0.090596	1.978734	-0.114317
Solidago uliginosa	2.845745	-0.104700	-1.76156	0.100795
Calamagrostis canadensis	0.976729	0.123528	-1.49355	0.000000
Eleocharis erythropoda	-43.2143	1.180751	4.371383	0.000000
Muhlenbergia glomerata	-6.96091	0.290756	2.111017	0.000000
Poa palustris	-0.502231	0.240713	5.869105	-0.368757
Rhynchospora fusca	-1.91634	0.251162	5.552589	-0.373081
Typha spp.	12.32279	-2.07774	-10.5999	1.712093
Cornus stolonifera	2.107478	-0.148510	-2.59464	0.179220
Rhamnus alnifolia	9.740856	-0.829460	-2.20125	0.104585
Rubus pubescens	-1.24094	0.081928	1.746250	0.000000
Salix candida	3.704028	-0.267219	-0.722762	0.196615
Salix pedicellaris	1.024854	0.084239	-0.157394	0.000000
Salix petiolaris	0.957835	-0.031764	1.381096	0.000000

App. 5.1. cont.

Bulk Density (g cm^{-3})

Species	a	b	c	d
Carex aquatilis	-0.449571	4.445730	-0.743518	0.000000
Carex flava	2.700166	-24.3731	1.041100	0.000000
Carex lacustris	4.524407	-27.7805	0.575859	0.000000
Carex lasiocarpa	0.328448	13.33355	0.861125	0.000000
Carex livida	-2.55128	23.75249	1.066981	0.000000
Carex stricta	-0.368033	3.520735	-0.458171	0.000000
Eupatorium maculatum	1.494431	-14.3465	1.452262	0.000000
Lycopus uniflorus	0.478252	3.230163	0.316319	0.000000
Lysimachia thyrsiflora	0.423208	-8.88702	2.348740	0.000000
Mentha arvensis	6.725991	-34.9519	0.294491	0.000000
Menyanthes trifoliata	2.519493	-15.6762	-5.93548	48.06285
Solidago uliginosa	0.462582	1.083744	0.741613	0.000000
Calamagrostis canadensis	-0.065487	6.254105	1.999198	0.000000
Eleocharis erythropoda	2.142944	11.14432	0.836981	0.000000
Muhlenbergia glomerata	1.161448	1.281478	1.044190	0.000000
Poa palustris	2.063100	5.053842	1.727703	0.000000
Rhynchospora fusca	-45.3841	254.4668	3.372874	0.000000
Typha spp.	0.469616	23.08576	-0.785013	0.000000
Cornus stolonifera	0.961175	-1.65635	0.050556	0.000000
Rhamnus alnifolia	542.0871	-3811.74	-0.251368	0.000000
Rubus pubescens	3.630706	-10.5135	-0.192156	0.000000
Salix candida	-2.18973	33.47965	1.439458	0.000000
Salix pedicellaris	0.294566	12.50798	0.527208	0.000000
Salix petiolaris	2.053654	-4.92859	0.361203	0.000000

App. 5.1. cont.

Dissolved Inorganic Nitrogen (mg L^{-1})

Species	a	b	c	d
Carex aquatilis	-0.204905	0.601186	-0.905119	0.000000
Carex flava	-0.058360	0.620755	0.394351	0.000000
Carex lacustris	0.055580	5.033378	-2.67484	0.000000
Carex lasiocarpa	1.779152	0.152507	1.126361	0.000000
Carex livida	0.527692	1.954104	-1.20651	0.000000
Carex stricta	0.985584	-1.13326	-0.898451	0.000000
Eupatorium maculatum	0.853449	0.216737	-0.005905	0.000000
Lycopus uniflorus	2.009974	-1.57063	-0.407952	0.864170
Lysimachia thyrsiflora	0.527765	-0.718192	1.897981	0.000000
Mentha arvensis	-0.486442	0.938389	1.404852	0.000000
Menyanthes trifoliata	-0.712645	1.290013	0.869573	0.000000
Solidago uliginosa	-0.269043	-1.11965	1.674411	0.000000
Calamagrostis canadensis	2.181136	-0.985124	1.337621	0.000000
Eleocharis erythropoda	1.068774	6.553720	0.189243	0.000000
Muhlenbergia glomerata	4.444282	-17.6878	2.089554	0.000000
Poa palustris	2.974529	-20.0019	4.388283	0.000000
Rhynchospora fusca	-1.24745	-2.32319	3.295441	0.000000
Typha spp.	1.176615	-4.86833	2.797946	0.000000
Cornus stolonifera	1.761249	-2.23185	0.913464	0.000000
Rhamnus alnifolia	-6.18184	3.978248	0.532988	0.000000
Rubus pubescens	2.599503	-3.24139	1.714107	0.000000
Salix candida	-164.272	133.9904	3.565685	0.000000
Salix pedicellaris	0.722285	-0.658583	2.063580	0.000000
Salix petiolaris	1.206876	0.055986	0.790001	0.000000

App. 5.1. cont.

Phosphate-P (μg L^{-1})				
Species	a	b	c	d
Carex aquatilis	-0.921170	0.016259	1.126550	-0.050657
Carex flava	-0.355153	0.078299	-0.251252	0.000000
Carex lacustris	-2.35796	0.332664	-4.86259	0.000000
Carex lasiocarpa	1.563992	0.026835	1.115076	0.000000
Carex livida	9.865079	-0.529061	-5.97201	0.297193
Carex stricta	0.024241	0.016757	-1.29597	0.000000
Eupatorium maculatum	-15.0397	-0.038276	-2.55823	0.346748
Lycopus uniflorus	1.247793	0.005428	-0.000949	0.000000
Lysimachia thyrsiflora	1.353166	0.047741	-0.133047	0.000000
Mentha arvensis	-13.2017	1.139360	2.409155	-0.197280
Menyanthes trifoliata	1.168062	0.016640	33.43385	-2.43640
Solidago uliginosa	0.726571	0.017388	0.340028	0.000000
Calamagrostis canadensis	2.562470	-0.046482	1.182360	0.000000
Eleocharis erythropoda	4.416816	-0.093270	0.293110	0.066480
Muhlenbergia glomerata	7.712725	-0.265756	-3.24150	0.128626
Poa palustris	121.8354	-14.9395	4.595120	0.000000
Rhynchospora fusca	-2.93042	0.155867	8.449810	-0.304230
Typha spp.	1.741007	-0.038254	2.162324	0.000614
Cornus stolonifera	-0.102382	0.002277	0.781196	0.000000
Rhamnus alnifolia	-204.327	7.383783	1.166413	0.000000
Rubus pubescens	-2.91017	0.119873	5.944682	-0.206910
Salix candida	-5.38587	0.292425	12.51082	-0.617234
Salix pedicellaris	0.199894	0.029803	3.286365	-0.075363
Salix petiolaris	1.194563	-0.001555	0.929816	0.000000

App. 5.1. cont.

Potassium-P (mg L^{-1})

Species	a	b	c	d
Carex aquatilis	2.079968	-1.22085	-2.08331	0.768374
Carex flava	0.234762	0.488370	-0.546811	0.000000
Carex lacustris	-108.935	78.21201	0.322784	0.000000
Carex lasiocarpa	2.458623	0.201158	-0.043363	0.000000
Carex livida	4.412713	-1.67184	1.287511	0.000000
Carex stricta	-4.25094	2.530332	0.150488	0.000000
Eupatorium maculatum	-16.2412	14.13388	9.460979	-9.53591
Lycopus uniflorus	0.834415	0.556035	-0.396196	0.000000
Lysimachia thyrsiflora	1.199250	0.188491	0.695041	0.000000
Mentha arvensis	0.575020	1.328655	-1.96877	0.000000
Menyanthes trifoliata	4.476253	-1.62458	-0.958462	0.544591
Solidago uliginosa	-1.51811	1.291168	3.262238	-1.77431
Calamagrostis canadensis	2.955361	0.024379	-1.20576	0.000000
Eleocharis erythropoda	5.756825	-5.44475	4.184590	0.000000
Muhlenbergia glomerata	4.546955	-0.789539	-0.674594	0.000000
Poa palustris	4.053719	0.415485	-1.26907	0.000000
Rhynchospora fusca	36.13680	-13.0625	2.750384	0.000000
Typha spp.	3.515869	-0.969390	0.079346	0.000000
Cornus stolonifera	0.925068	-0.303449	0.271781	0.000000
Rhamnus alnifolia	-3.74528	1.206974	19.65801	-8.60964
Rubus pubescens	3.395618	-1.81053	1.952917	0.000000
Salix candida	5.163127	-0.731071	-1.32434	0.000000
Salix pedicellaris	2.461524	-0.244314	0.045398	0.000000
Salix petiolaris	-52.3907	26.43907	1.810196	0.000000