Characterizing Spatial and Temporal Variations in Nutrient and CO$_2$ Dynamics Within and Across Peatlands in the Western Boreal Plain, Canada

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Peatlands are found extensively throughout the Western Boreal Plain, a region under pressure due to persistent drought conditions and industrial development (especially oil and gas, and oil sands development). Our ability to predict peatland responses to these stressors is hampered by a lack of scientific understanding of natural biogeochemical processes, such as nutrient and CO_2 dynamics in peatlands in this region, and, the drivers of these processes. An understanding of the natural spatial and temporal variation in nutrient and carbon dynamics within and among peatland systems and the interactions between the two is needed. This information can then be used to develop successful reclamation and best management practices during oil industry related development.

This thesis is comprising two studies characterizing nutrient dynamics within the Athabasca Oil Sands region (AOS) of Alberta. The first study simultaneously examined and compared nutrient (nitrogen, N and phosphorus, P) dynamics (extractable pools, net transformation (mineralization) rates and supply rates) and rates of terrestrial CO_2 exchange within a poor fen (JACOS) throughout the growing season of 2012 to characterize seasonal patterns in nutrient and carbon dynamics and determine if relationships existed between these. A second objective of the first study was to determine if a semi-permanent road constructed across the fen that obstructed the natural flow of groundwater, impacted nutrient and CO_2 exchange processes The second study focused on the peak growing season and compared nutrient dynamics between the JACOS site and four additional peatlands that fell along an apparent hydrologic and minerotrophic gradient.

Results suggest that both nutrient dynamics and CO_2 exchange varied temporally throughout the season with maximum transformation/exchange rates (net mineralization, NEE) in peak summer (June, July) as a consequence of warm temperatures, and reduced rates of biogeochemical exchange during the cooler shoulder seasons. Direct statistical relationships between carbon and nutrient dynamics were not apparent in the data set, although N and CO_2 exchange processes appeared to be generally affected by similar environmental drivers, although the specific drivers of individual N, and CO_2 exchange processes were variable. For example, C exchange processes in JACOS were driven by a combination of temperature, photosynthetically-active radiation (PAR) and moisture. In contrast, N availability appeared to be driven largely by external supply and to a lesser extent, internal mineralization that was driven primarily by temperature. In contrast, P appeared to be a function of hydrologic (and apparent redox) conditions within this site. Although, the road had significant impacts on moisture and water table depths, this did not result in substantial impacts to either N or CO_2 dynamics within this fen, likely because the moisture differences on either side of the road were not significant enough to lead to a biogeochemical response. Collectively, these results demonstrate that different types of natural (seasonal, climatic) and anthropogenic stresses impact biogeochemical processes in different ways in this landscape.

Findings from the second study determined that nutrient (N and P) content in the WBP does not follow a geochemical gradient. The drivers of N and P across the five sites were similar to those found at JACOS, where N was largely driven by external supply and P was driven by redox conditions. In general, nutrient content was comparable across different peatland types with the

exception of JACOS, where on-site contamination most likely resulted in greater nitrate and P content.

Biogeochemical cycles in the WBP are complex. Our studies determined that there is not one single driver that controls N, P and CO_2 dynamics within this landscape, and demonstrates that variable hydrology affects biogeochemical cycles in different ways. This finding complicates recommendations for reclamation projects as managers may be forced to optimize for a given biogeochemical cycle. In the WBP, nutrient dynamics did not appear to vary along a hydrologic gradient, suggesting that the moisture thresholds required to affect nutrient cycles are greater than what has been shown for carbon.

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Chapter 1

Introduction

Brief Rationale

Peatland ecosystems are important to the global carbon (C) (Gorham, 1991; Loisel *et al.,* 2014) and nitrogen (N) budgets (Wray and Bayley, 2008; Loisel *et al.,* 2014). Recent literature has focused on C cycling within these systems but less is known about N dynamics (Bridgham *et al.,* 1996) and the inter-relationships between the two. These relationships are important in understanding how nutrients, specifically nitrogen and phosphorus (P) affect plant production, carbon exchange and peat accumulation within peatlands. The knowledge gap in C and nutrient relationships can be attributed to the limited knowledge on N and P cycling within peatland ecosystems, where quantifying the inter-couplings involved in driving nutrient dynamics is difficult to achieve in the field (Kellogg and Bridgham, 2003). Heterogeneity within and among peatlands further complicates the understanding of biogeochemistry in these systems.

Characterizing the main drivers of C, N and P dynamics in peatland ecosystems is necessary in determining the relationships among carbon and nutrients and also essential to predicting how these environments will respond to natural and anthropogenic changes. Predicting the effects of disturbances on peatlands is particularly important in the western boreal plains (WBP) of northern Alberta, Canada, where peatland ecosystems are under threat due to climate change and oil development (Graf, 2009).

Disturbances to western boreal forests are common and have shaped the ecological function of these ecosystems. However, these disturbances in the past have been the cause of natural disruptions such as fire and insect outbreaks (Turetsky and St. Louis, 2006). Currently, much of the WBP terrain has been altered by anthropogenic disturbances including, but not exclusive to oil development in the Athabasca Oil Sands (AOS) region of Alberta, Canada. Unfortunately, much of the research related to disturbances in boreal ecosystems has been focused on upland systems and not on lower terrain such as peatlands (Turetsky and St. Louis, 2006).

As a means to balance the damage related to oil development, the government of Alberta has enforced the industry to reclaim decommissioned oil sands (Rooney *et al.*, 2012). Reclamation has been described as changing unproductive landscapes to a more usable, productive state (Clewell and Aronson, 2007), whereas restoration practices focus on bringing a disturbed ecosystem back to its natural and original ecological function (SER, 2004). The goal in peatland restoration in North America has focused on returning disturbed sites back to peat accumulating ecosystems, where nutrient dynamics and plant communities return to their pre-disturbed status (Rochefort, 2000). However, the current policies do not enforce the oil industry to restore post-mined peatlands (Government of Alberta, as cited in Rooney *et al.*, 2012) but instead companies are able to reclaim disturbed areas into ecosystems that can be characterized as productive (Foote, 2012). The guidelines characterizing the best reclamation practices are vague or non-existent and recent literature has suggested that constructing and/or restoring a peatland is unachievable due to constraints on time, area and limited knowledge on how these ecosystems naturally function (Foote, 2012). For example, it has been suggested that the first step in restoring a

wetland should be to return the hydrology of a landscape back to its original hydrologic function (Mitch and Gosselink, 2000). Indeed, there are vast amounts of literature on the hydrology of wetland and peatland systems (Siegel & Glaser, 2006) and restoring the hydrology in wetland systems has been accomplished in some settings (Price *et al.*, 2003). However, specific knowledge on the hydrologic function of peatlands in the WBP is limited. This knowledge is essential to the development of better reclamation and restoration practices (Ferone and Devito, 2004). Consequently, the majority of post-mined peatlands are being reclaimed into upland forests (Rooney *et al.*, 2012).

Contrary to the aforementioned issues, there have been success stories in peatland reclamation. The restoration of cutover peatlands has been researched for over 15 years (Rochefort *et al.*, 2003) and many of these practices could be applied to the restoration of linear disturbance and post-mined areas by the oil industry (Graf, 2009). Furthermore, the addition of fertilizer in the reclamation of Alaska's North Slope has contributed to the success in revegetation (Peterson, 2001). These few examples combined with current and future research on peatland function and reclamation practices suggest that constructing a successful reclamation peatland in the AOS is not as unattainable as previously implied.

The knowledge gap of western boreal peatland function can be reduced through studying nutrient dynamics within and among different peatland types and determining important relationships among nutrients and carbon. Quantifying the biogeochemistry of WBP peatlands can be used to develop best management and successful reclamation practices. The goal of this thesis is to understand hydrological and seasonal controls on biogeochemical processes in WBP peatlands, which can then be applied to reclamation practices.

The following sections of this Chapter will discuss the study objectives of each manuscript and a literature review that will focus on the general knowledge of peatland function, the biogeochemical processes related to N, C and P and briefly describe how oil industry related disturbances, such as roads and well pads affect these processes.

Study Objectives

This thesis characterizes nutrient (N and P) and carbon dioxide (CO_2) dynamics in western boreal peatland(s) within the AOS. Variations in nutrient dynamics were examined across different peatland types, comprise natural and disturbed fens and bogs. The main site was linearly disturbed by a semi-permanent road and was studied to determine spatial and temporal variations in nutrients and CO_2 exchange and used to examine the impact a semi-permanent road has on these dynamics (Chapter 3). Examining nutrient dynamics within and across different peatlands determined if nutrient content varied according to differences in moisture and or mineral content of different peatland types (Chapter 4).

The objectives of this thesis are to (1) determine if spatial and temporal variation in N, P and CO_2 dynamics exist within a WBP peatland (2) determine if there are relationships between N and ecosystem productivity (CO_2 exchange); (3) and to determine the effects of a road on nutrient dynamics and CO_2 exchange within a peatland ecosystem (Chapter 3);(4) and determine if similar spatial trends in nutrient dynamics exist across different peatlands that fall along an apparent moisture and minerotrophic gradient. These objectives will provide an understanding on how linear disturbances directly affect nutrient dynamics and CO_2 exchange in a peatland ecosystem and fill in the knowledge gap on how nutrients function across a range of WBP peatlands.

It is hypothesized that: (1) general seasonal trends will be found in N, P and CO_2 dynamics, where nutrient supply rates and productivity will peak late in the growing season; (2) based on the findings of Eppinga *et al.* (2008), nutrient variation between microforms is expected, where hummocks will have greater P and N supply and we expect to find greater vascular biomass in hummocks resulting in greater uptake of CO_2; (3) significant relationships between N and CO_2 will exist, where N supply can be used to predict the productivity of a system; (4) the road will have impacts on N dynamics, causing lower N supply on the wetter side of the road, which in turn will result in lower rates of productivity (GEP) and respiration. Ultimately, this information can be applied to BMPs and reclamation projects in AOS, as suggested in Chapter 5.

Literature Review

General Overview of Peatlands and Significance to the Western Boreal Plain

Peatlands are important ecosystems in the western boreal plain (WBP) of Canada, where they cover 31% of the western boreal forests of Northern Alberta (Vitt *et al.*, 1995). Peatlands are a type of wetland characterized by having a peat layer depth > 40 cm (National Wetlands Working Group, 1997). Peat is organic matter that develops as a result of slow decomposition rates typically observed in poorly drained soils with high water levels having anaerobic and cool conditions (Gorham, 1991; Halsey et al., 1997). The rate at which peat is accumulated is dependent on the balance between C sequestered through primary production and the loss of C to decomposition of organic matter (Clymo, 1984; Aerts *et al.*, 1995).

The hydrologic function of peatlands is not only an important control on peat accumulation but is also key in forming the spatial heterogeneity observed within and among peatlands. For example, peatlands have two main layers divided by differences in soil moisture conditions (Daniels *et al.*, 2008). The acrotelm is the upper layer and is characterized by its variable soil moisture levels caused by fluctuating water table and relatively high hydraulic conductivity. It comprises mostly bryophytes and a thick layer of organic litter (Hasley *et al.*, 1997). The lower layer is the catotelm, which is under anaerobic conditions due to high water levels resulting in waterlogged environments. Peat accumulation is dense having slightly lower porosity and hydraulic conductivity (Daniels *et al.*, 2008). Natural spatial variability in peatland hydrology exists in microtopography. Hummocks form topographic highs in peatlands and have a greater acrotelm due to the vertical growth of *Sphagnum* spp.; most commonly *Sphagnum fuscum*. Hollows are depressions in the peat surface and are commonly waterlogged and are covered by S*phagnum angustifolium* (bogs) (Hayward & Clymo, 1982) as well as other species (fens).

The majority of peatland research has been committed to understanding the ecology of these systems. Many of these studies have long-established that there is a strong relationship between hydrology and ecology, where their interactions influence the function of peatland systems (Siegel & Glaser, 2006). The inter-relationships among the hydrogeology, climate and biota have been used to define and classify different peatland types (Bridgham *et al.*, 1996), where two distinct classes of peatlands are widely acknowledged throughout the literature: (1) Fens and (2) Bogs (Halsey *et al.*, 1997; Quinton *et al.*, 2003).

Fens are minerotrophic as they can receive water from two main sources: one being mineral sourced water from external water bodies and the other through precipitation. The topography and hydrologic function of fens can differ and fens can be further characterized as: (1) geogenous fens, which develop on flat, concave or sloping terrain (NWWG, 1997) and are distinctly covered by a large percentage of bryophytes (Bridgham *et al.*, 1996); and (2) topogenous peatlands develop in a depression and receive water from a single outlet, which is most likely groundwater (Bridgham *et al.*, 1996). These fens are also characterized by a relatively stable water table (Rydin and Jeglum, 2006); (3) limnogenous peatlands are located near bodies of water such as lakes or low flowing streams (Bridgham *et al.*, 1996; Rydin and Jeglum, 2006); and can be periodically flooded by the adjacent water systems (Rydin and Jeglum, 2006) and (4) soligenous peatlands develop on a slope and receive external sources of water through or over the peat surface (Bridgham *et al.*, 1996; Rydin and Jeglum, 2006). Characterizing fens on the pH, ion concentrations and chemistry is common in literature and they are often referred to as rich or poor. Fens having a pH of 7 or higher due to elevated bicarbonate and calcium contents are defined as being alkaline and rich. Rich fens are also found to have a greater diversity of vascular plant species relative to poor fens and are predominately covered with brown mosses (Zoltai and Vitt, 1995). In contrast to this, poor fens are acidic, have low vascular plant diversity, are dominated by *Sphagnum* moss and in general, have similar chemical and plant characteristics as bogs (Zoltai and Vitt, 1995).

Bogs are ombrotrophic and also ombrogenous meaning water can only be received from the atmosphere via precipitation (Bridgham *et al.*, 1996; Halsey *et al*, 1997; Quinton *et al.*, 2003). They are located on flat, raised or sloping terrain and have a water table

position below or level with the surface (NWWG, 1997; Rydin and Jeglum, 2006). The negligible influx of mineral sourced water causes bogs to have a lower mineral content than fens and are therefore more acidic having a pH range of 4 – 4.8. The acidic environment limits the growth of many vascular plant species but is favourable for *Sphagnum* mosses (NWWG, 1997). However, bogs with a low water table and dry, aerobic conditions have been found to have plant communities comprising ericaceous shrubs, dwarf shrubs and lichens (Zoltai and Vitt, 1995).

Plant Productivity and Terrestrial CO$_2$ exchange in Boreal Peatlands

The carbon balance of an ecosystem is dependent on the difference between primary production and decomposition rates (Silvola *et al.*, 1996; Schlesinger, 1997). The balance is unique in peatland systems, where large amounts of C are stored in peat due to low decomposition rates as an effect of several hydrological and environmental factors including high water levels, anaerobic conditions and cool temperatures (Clymo, 1984; Gorham, 1991). Boreal peatlands have been determined to hold one-third of the world's soil carbon (Gorham, 1991). Consequently, the WBP is important to the global C budget. This section will briefly review terrestrial carbon exchange and the abiotic and biotic controls of productivity, respiration and decomposition in the WBP peatlands.

Primary production has been suggested to be one of the most important factors in peatland function for the inputs of plant organic matter are necessary for peat accumulation and therefore carbon sequestration. In the boreal region, conditions are favorable for peat accumulation, where peatlands have produced vast amounts of peat over the last 5,000 to 7,000 years (Wieder, 2006). It is well known that peatlands store a lot of

soil carbon (C) and it has been estimated that an average of 1.5% of this C remains in vegetation (Rochefort *et al*., 1990; Blodau, 2002) whereas over 98.5 % of C is stored within the acrotelm and catotelm (Gorham, 1991). However, this storage is highly variable as CO_2 uptake by photosynthesis and CO_2 release via decomposition and respiration varies spatially with microtopography within peatlands and seasonally (Aerts and Ludwig, 1997). The fluctuations in carbon storage can be estimated by determining the terrestrial exchange of CO_2. In this thesis, the carbon exchange is simplified by omitting methane and dissolved organic carbon (DOC):

$$NEE = GEP + R_{tot} \tag{1}$$

where, NEE is net ecosystem exchange, which is the change in carbon storage (g $C/m^2/d$). GEP (gross ecosystem production) is the amount of CO_2 uptake by plants and represents primary productivity of an ecosystem. R_{tot} is the release or loss of CO_2 from an ecosystem by plant respiration, plant roots and decomposition by microorganisms (Solondz, 2007).

Current research on gross primary production and photosynthesis has found that primary production is positively correlated with photosynthetically active radiation (PAR), nutrient availability, water table position (Szumigalski and Bayley, 1997; Chivers *et al.*, 2009), temperature (Blodau, 2002; Chivers *et al.*, 2009) and vegetative biomass (Chivers *et al.*, 2009). However, knowledge gaps in characterizing the main drivers of peatland productivity remain because estimating ecosystem production is difficult as different vegetation forms can respond differently to changing environmental variables (Szumigalski and Bayley, 1997). Consequently, limited studies in boreal peatlands have estimated the productivity of whole ecosystems and instead many studies have solely focused on the productivity of *Sphagnum* mosses, where findings suggest that temperature

and precipitation are the main drivers of productivity in *Sphagnum* spp. (Wieder, 2006). One of few studies looking at productivity in vascular species found that water table position and phosphorus (P) content had the greatest effect on vascular plant productivity in fens suggesting that boreal fens could be P limited (Thormann and Bayley 1997).

The rate of ecosystem photosynthesis is balanced by respiration (plant and soil) and decomposition. Plant respiration is the metabolism of vegetation and has been determined to increase with temperature, biomass, N content (Schlesinger, 1997), water table depth and growth period (Chivers *et al.*, 2009). Decomposition rates are driven by temperature, water level, aeration and microbial activity (Silvola et al., 1985 as cited in, Silvola *et al.*, 1996; Blodau, 2002). Decomposition also has a direct correlation with temperature (Moore and Knowles, 1989). The microbial activity needed to break down organic matter has been found to have a Q_{10} of 2 (Edwards, 1975, as cited in Schlesinger, 1997). In general, carbon exchange in peatlands is driven by the coupling and inter-relationships between temperature and soil moisture, water table position and nutrient availability (Bonan and Van Cleve, 1992; Silvola *et al.*, 1996; Chivers *et al.*, 2009; Cai *et al.*, 2010). For example, increased seasonal temperatures have been determined to elevate rates of evapotranspiration (ET) and decrease water table position and soil moisture (Chivers *et al.*, 2009), which in turn promote the release of CO_2 (Silvola *et al.*, 1996).

Variability in C exchange within peatlands has also been linked to an ombrotrophic-minerotrophic gradient where poorer, ombrotrophic sites covered with *Sphagnum* mosses were found to emit lower rates of CO_2 than richer, *Eriophorum vaginatum* (tussock cotton grass) and shrub covered peatlands (Silvola *et al.*, 1996). Furthermore, elevated nutrient availability can increase productivity (Bonan and Van

Cleve, 1992; Updegraff *et al.*, 1995; Mack *et al.*, 2004). The higher rates of decomposition and respiration can sometimes exceed rates of production transforming peatlands from a carbon sink to source (Mack *et al.*, 2004). This has been observed in poor soils common to open peatlands of the WBP, where nutrient resorption has been linked to high levels of respiration (Solondz *et al.*, 2008) and when excess nutrients cause a shift in microbial communities resulting in an increase in decomposition rates (Blodau, 2002).

Nitrogen Dynamics in Peatlands

Western boreal peatlands are important to the global N budget. Similar to the carbon cycle, large amounts of N are stored in the WBP (Wray and Bayley, 2007). Indeed, N has been suggested to be a critical factor in the overall function of peatlands however, little research has been devoted to understanding the complex interactions of nutrient dynamics (specifically N and P) in peatland ecosystems (Bridgham *et al.*, 1996). Characterizing N dynamics are difficult to determine in field studies, for example, recent studies have found measuring plant uptake challenging due to low rates of mineralization commonly found in northern peatlands (Weintraub and Schimel, 2005). Moreover, the effects of anthropogenic disturbances complicate the understanding of N dynamics in peatlands. For example, peatland drainage and increased N deposition can lead to more obscure findings that differ from results determined in undisturbed systems (Limpens *et al.,* 2006).

Although, there are many gaps in the literature regarding nutrient dynamics in northern boreal peatlands, much research has been conducted in temperate regions and can be used to extrapolate the processes involved in N dynamics in the western boreal region. This section will briefly review the N cycle in peatlands and discuss the biotic and abiotic

controls.

Available N can enter a peatland system via N fixation, external upland runoff and atmospheric deposition (Turetsky, 2003; Limpens *et al.,* 2006). Biological N fixation is an enzyme-catalyzed process where atmospheric N (N_2) is reduced to inorganic and plant available ammonium (NH_4^+) and nitrate (NO_3^-) (Jacobson *et al.*, 2000) and is the greatest source of available N in most ecosystems (Turetsky, 2003). The reaction requires a large amount of energy ($\sim$ 940 KJ/mol) to break the N bond of N_2 to form NH_4^+ and ammonia (NH_3) (DeLuca *et al.*, 2000). Free-living microorganisms composed of nitrogenase enzymes use oxygen to break the triple bond of N_2 (Jacobson *et al.*, 2000). In peatlands, these microorganisms include bacteria, cyanobacteria and *actinomycetes spp.* (Rydin and Jeglum, 2006). Bacteria including *Nitrosamonas* and *Nitrobacter* are decomposers (DeLuca *et al.*, 2000) that live in organic matter and can tolerate anaerobic conditions. They fix the majority of N in ombrotrophic and acidic peatlands (Granhall and Selander, 1973, as cited in Limpens *et al.,* 2006). Cyanobacteria and *actinomycetes* form symbiotic relationships with fungi, mosses and vascular plants (DeLuca *et al.*, 2000) and favour wetter, more alkaline and minerotrophic peatlands (Steward, 1974, as cited in Limpens *et al.,* 2006) but have been found to live in the wet hollows of more acidic, ombroptrophic bogs. These microorganisms can fix N in one of two pathways: (1) ammonia assimilation: the process of an organism taking up inorganic nitrogen compounds (NH_4^+ or NH_3) to become part of its biomass and (2) ammonification and nitrification.

Ammonification is a process where organic forms of N form NH_4^+ and NH_3. The process can be simplified into 3 consecutive steps: (1) soluble N forms are leached from detritus (2) microbes immobilize the leached N and (3) excess N can be mineralized once

C:N ratios in peat surpass the ratio essential to microbial growth (Aerts and Champin, 2000, as cited in Limpens *et al.*, 2006) (approximately 30)(Schlesinger, 1997). Following ammonification, a second N fixing step can be carried out, known as nitrification. Nitrification is an energy intensive aerobic process where NH_4^+ and NH_3 react with oxygen to form nitrate (NO_3^-) and nitrite (NO_2^-) and can be characterized in two steps (Jacobson *et al.*, 2000):

$$NH_4^+ + 3/2\ O_2 \rightarrow NO_2^- + H_2O + 2H^+ \tag{2}$$

$$NO_2^- + \tfrac{1}{2}\ O_2 \rightarrow NO_3^- \tag{3}$$
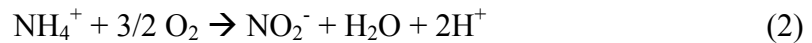
Nitrogen fixation has been found to increase with peat moisture (Davey and Marchant, 1983, as cited in Limpens, *et al.,* 2006), temperature, redox potential, alkalinity, potassium (K) and P levels and decline with calcium (Ca) content (Waugham and Bellamy, 1980, as cited in Limpens, *et al.,* 2006). Ammonification and nitrification rates are controlled by coupled relationships between site-specific hydrology with ambient and soil temperatures, soil moisture and aeration (Updegraff *et al.*, 1995; Bridgham *et al.,* 1998; Jonasson and Shaver, 1999; Keller *et al*, 2004; Rydin and Jeglum, 2006). For example, higher temperatures increase microbial activity leading to greater rates of ammonification and nitrification (Bonan and Van Cleve, 1992; Updegraff *et al.,* 1995; Mack *et al.*, 2004). Moisture conditions have a strong effect on ammonification and nitrification rates as mineralization increases with oxygen availability and lower water levels (Keller *et al.*, 2004). Furthermore, decomposing and nitrifying bacteria are inhibited in peatlands with water levels above or near the surface resulting in lower N availability and greater denitrification rates (Rydin and Jeglum, 2006). Alkalinity can also affect

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nitrification rates, as nitrifying bacteria become less active in more acidic peatlands (pH <5) (Bayley *et al.*, 2005).

Vegetation uptake is characterized by the rate of nutrient diffusion from soil to root. Uptake of ammonium and nitrate is most likely rapid in peatlands as a result of low N availability (Schlesinger, 1997). Consequently, many species of peatland vegetation developed adaptations to acquire the sufficient amount of N necessary for growth and survival. For example, several vascular species in N-limited environments have been found to assimilate N directly from amino acids (Chapin *et al.*, 1993) and bryophytes, in particular have a morphological advantage as they do not have stomata or an effective cuticle allowing free exchange of gas and solutes across the plant cells (Turetsky, 2003). This provides bryophytes with the ability to trap nutrients found in precipitation (Jonasson and Shaver, 1999; Turetsky, 2003) and receive nutrients from pore water within the capillary zone. (Limpens *et al.,* 2006). As a result, bryophytes specifically *Sphagnum spp*. have become great competitors by rapidly immobilizing and limiting available N to surrounding plant and microbial species (Zoltai and Vitt, 1995; Jonasson and Shaver, 1999).

If N is not assimilated or immobilized by plants and microbes, it can be lost or removed from peatland systems through a reduction process known as denitrification. Denitrification removes inorganic N from biological systems by reducing nitrates to any gaseous nitrogen species, which are then released into the atmosphere (Jacobson *et al.*, 2000). Denitrification rates are controlled by moisture conditions and NO_3^- content, where peatlands having excess NO_3^- are expected to have elevated rates of denitrification. It has been suggested that rich and drier fens will have greater NO_3^- content than bogs, poor fens

and waterlogged peatlands and therefore drier, rich peatlands will have greater denitrification rates (Martikainen, 1993, as cited in Limpens *et al.*, 2006).

Phosphorus Dynamics in WBP Peatlands

Similar to nitrogen, phosphorus is an essential component in peatland function. However, the controls and relationships of P dynamics in peatlands are not well understood and even less is known about P than N in northern and boreal peatlands. The difficulty in understanding the controls of P dynamics is related to quantifying the complex inter-relationships between the geochemical and biotic factors in P cycling (Bridgham *et al.*, 2001, as cited in Kellogg and Bridgham, 2003). Throughout this section the P dynamics in peatlands will be briefly reviewed.

Phosphorus comes from the weathering (physical, biological and chemical) of calcium phosphate minerals (Schlesinger, 1997). Primary and secondary minerals important to P availability are created through the weathering of apatite, a form of calcium phosphate and include iron (Fe), aluminum (Al), manganese (Mn), calcium (Ca) and magnesium (Mg) (Lindsay *et al.*, 1989, as cited in Walbridge & Navaratnam, 2006). P is commonly bound to these minerals, where in acidic environments the reaction of phosphate ions (precipitation) with Fe, Al and Mn are particularly important in controlling P availability. In alkaline environments, precipitation of Ca and Mg influence P availability (Schlesinger, 1997). Nevertheless, P is occluded or unavailable when bound to the oxide forms of these secondary minerals. P can become non-occluded or available through anion adsorption reactions (Schlesinger, 1997). However, peat accumulation inhibits the connection between the underlying mineral soil and the upper, surface layers

of organic peat. As a result important secondary elements such as Fe and Al are organically bound and unavailable for plant use (Walbridge & Navaratnam, 2006). Consequently, in boreal peatlands, P content is most likely controlled by biological weathering or other biological processes (Walbridge & Navaratnam, 2006). The importance of biological controls on P availability has been suggested to decrease along an ombrotrophic − minerotrophic gradient and geochemical controls are expected to have greater effects in fens having elevated mineral content (Mitsch and Gosselink, 2000).

Biological controls on P dynamics in peatlands have been reviewed in few studies, where Richardson and Marshall (1989) found that under natural conditions, microorganisms and adsorption were the most important factors increasing P availability. Microorganisms can control P dynamics by assimilating inorganic and organic P from soils. This can only be accomplished if the organisms have enzymes known as phosphatase (Vance *et al.*, 2003). The production and use of these enzymes increase with low soil available P (Malcolm, 1983, cited in Schlesinger, 1997) thus microbes can rapidly immobilize and limit P to nearby vegetation. Conversely, similar phosphatase enzymes have been found to exist on the mychorrizal fungi, which provide plants with available P (Vance *et al.*, 2003).

A more recent study suggests that microbes and plants contribute to P dynamics equally (Kellogg and Bridgham, 2003). The extent to which plants affect P dynamics is dependent on the species and stage of plant growth (Reddy & DeLaune, 2008). Bryophytes, for example have been found manipulating their environment by increasing the redox potential of shallow fens which caused increased soil and root phosphatase, elevated P supply and stimulated plant growth, root vitality and microbial activity

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(Crowley and Bedford, 2011). Moreover, the P content stored within a plant's biomass is a very important factor in P dynamics. Decomposition and leaching of plant-based detritus can rapidly release dissolved organic phosphorus (DOP) into peat and pore water. DOP can be mineralized by decomposition, where rates of mineralization have been found to increase with P content (C:P) (Reddy & DeLaune, 2008).

Hydrologic and geochemical controls on P dynamics include aeration (redox potential), soil content of phosphate ion receptors (Fe, Al, Mn, Ca, Mg) and ambient P content (Reddy & DeLaune, 2008). Aeration or redox potential could be one of the most important environmental factors regulating P availability in peatland ecosystems. Water level positions in peatlands are typically below the peat surface resulting in the upper layers to be aerobic (Moore *et al.*, 2005) with high redox potential. In such conditions, P can either be released via organic hydrolysis (Aldous *et al.*, 2005), decomposition or mineralization (Reddy & DeLaune, 2008). Conversely, when redox is high, P is bound to the oxyhydroxide flocs of ferric iron (Fe^{3+}) and is inaccessible for plant and microbial use. After a rise in water level, when the upper layers of peat become submerged in water, oxygen availability is limited and redox is lowered. The ferric form of iron is then reduced to a ferrous form (Fe^{2+}) and inorganic P is released (Aldous *et al.*, 2005), resulting in an influx of available P under flooded conditions.

The Effects of Linear Disturbance on WBP Peatlands

Open pit mines are not the only oil related disturbance in AOS. Other disturbances include pipelines, seismic lines, roads and well pads. Each can alter boreal wetlands through fragmentation, destruction of habitat, changes to local hydrology and contaminating

wetland water and soil (Graf, 2009). Although each disturbance is important in its own right, this section will focus on roads and well pads as it pertains to one of the study sites within this thesis.

Although roads have been found to cause more damage than pipelines and seismic lines (Turcheneck, 1990) the effects of roads on peatland ecosystems in the WBP are generally unknown. There are two types of roads that are typically developed in the energy sector (1) semi-permanent roads and (2) winter roads. Semi-permanent roads consist of two main layers, the first being a geotextile layer that is covered by mineral or clay soil (Jos Lussenburg, JACOS, as cited in Graf, 2009). Winter roads are less invasive as they do not compose of externally sourced soils and instead are used only when the natural ground cover is frozen (Graf, 2009). The development of roads changes the regional hydrology by obstructing groundwater flow (Devito and Mendoza, 2007; Turetsky and St. Louis, 2006) and altering the water chemistry (Turcheneck, 1990), which can affect peatland vegetation communities (Turcheneck, 1990; Turetsky and St. Louis, 2006).

Unlike roads, well pads are used for oil extraction and are a non-linear disturbance. They typically range from 1 to 10 ha, with layers of compacted peat or externally sourced fill and compose of a mineral or clay cap placed in or above the compacted layers (Opti Canada and Nexen, 2006, as cited in Graf, 2009). The development of pads alters the hydrology of an ecosystem and can contaminate adjacent peat and water through an oil spill or by mineral material leaching from the mineral cap (Graf, 2009).

The construction of roads and well pads compact the underlying peat which has significant effects on the regional hydrology including: draining and or flooding nearby areas, altering hydraulic conductivity, pore structure and water table fluctuations (Price *et*

al., 2003) and ultimately inhibit plant growth (Graf, 2009). Altering the water table could significantly affect the ecological function of a peatland because water level is a dominant driver in carbon and nutrient cycles and water table fluctuations can lead to a shift in plant and microbial communities (Macrae *et al.*, 2013).

Chapter 2

Research Approach and Study Sites Used

In this thesis, temporal and spatial variations in N, P and CO_2 dynamics within a poor fen throughout three months in the summer of 2012 were examined. The fen was located on the Japanese Canada Oil Sands site (JACOS) and was bisected by a semi-permanent road. This provided the opportunity to determine the direct impacts of a road on nutrient and carbon dynamics. Throughout the peak-growing season (July), nutrient dynamics across five peatlands were examined (one of which was the JACOS fen) to determine variations within and among different peatland types that fell along an apparent moisture and minerotrophic gradient. More detail on each site and a brief description of methods used to determine N, P and CO_2 dynamics are provided below.

Road-Impacted Site (JACOS)

Throughout the months of June to August 2012, research was conducted on a poor open fen located on a steam assisted gravity drainage oil sand (SAGD) site known as JACOS. The fen had a 450 m semi-permanent road constructed east to west in 2001. The road was perpendicular to the flow of water (north to south) and separates the fen into two sections: north of the road and south of the road. The site set up consists of six chamber plots on each side of the fen (Figure 2.1). Each plot has two collars (one installed in each microform) for CO_2 chamber measurements and one well. Each plot on the same side of the fen has similar species composition providing each side with six replicates. At each

chamber plot, bi-weekly CO_2 chamber measurements using a plexi-glass chamber and infrared gas analyzer (IRGA), groundwater samples and corresponding environmental variables were collected. Cores (10 x 10 x 10 cm) of the upper peat layer were collected once every three weeks for extractable N and P content and the buried bag method was used to determine net transformation rates (See Chapter 3). The results from the JACOS site were used to determine spatio-temporal trends in nutrients and C dynamics and to see if a relationship exists between N and C (objectives 1 and 2; Chapter 1). Additionally, the site determined the potential impacts a semi-permanent road has on N and C dynamics in WBP peatlands (objective 3; Chapter 1).

Additional Peatland Sites

Over the peak-growing season (3 weeks in July), N and P dynamics were characterized across 5 different peatland types in the AOS. The peatlands are comprised of natural and disturbed sites and had slight ombrotrophic-minerotrophic (as determined by vegetation and hydrology) and moisture gradients. The natural sites include a bog (Wandering River bog or WR N), and a treed rich fen (Poplar Creek fen or POP). The disturbed sites include the JACOS site, a poor fen Pauciflora (long term road effects) and a drained bog, where the water level was on average 70 cm lower than the natural bog (Wandering River drained site, hereafter referred to as WR D). Peat cores (10 x 10 x 10 cm) from hummocks and hollows were collected at each site and analyzed for extractable N and P pools. Corresponding cores were incubated for three weeks, following the buried bag method to determine net transformation rates (Chapter 4). The results from the 5 sites determined if there was spatial variability in nutrient dynamics in WBP peatlands and whether or not

nutrient content follows a hydrological or geochemical gradient this information is useful in limiting the knowledge gap on how peatlands in the AOS function (objectives 4 and 5; Chapter 1).
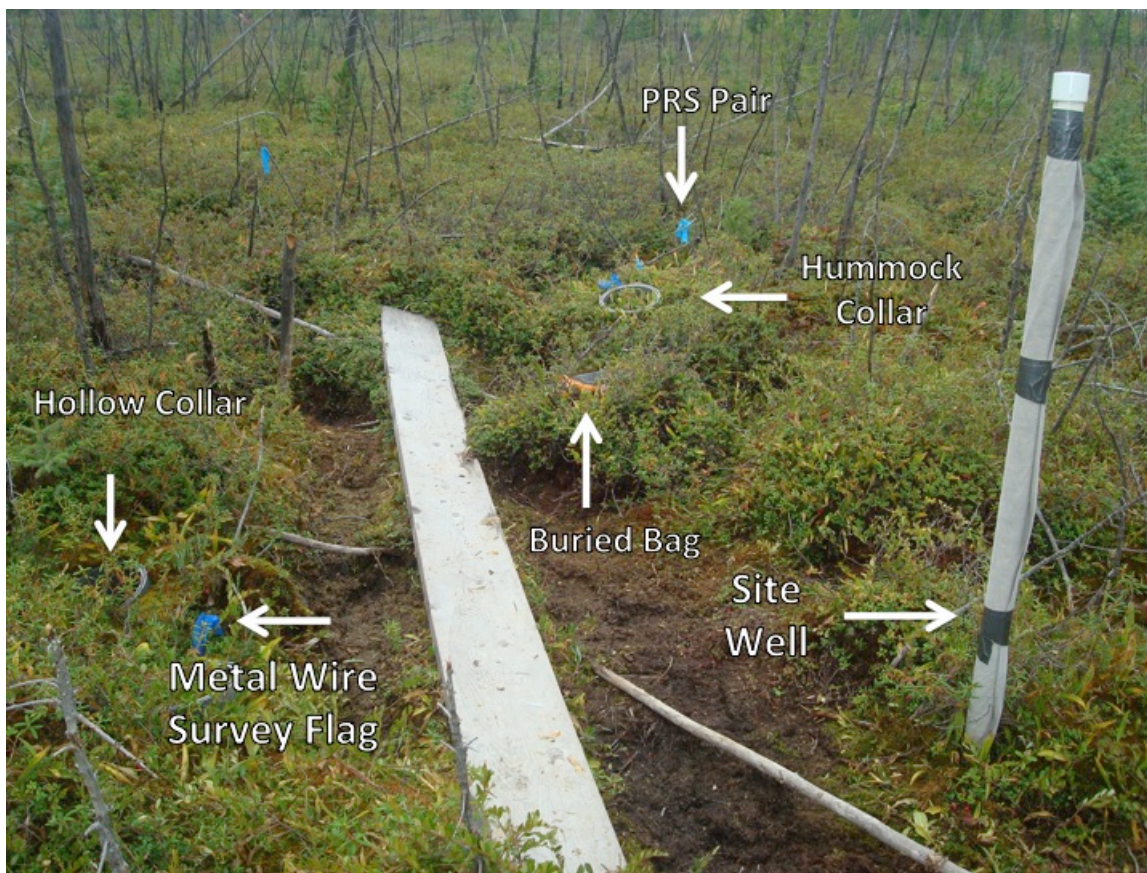
Figure 2.1: Community scale chamber site at JACOS fen. Each community scale chamber site had a 2x10 boardwalk, one well and 2 sets of the following: collars for chamber CO_2 measurements, metal wire flags for estimating redox potential, buried bags to estimate net transformation rates and peat cores used to determine ext-nutrient pools. One set was located in a hollow whereas the other was located in a hummock of each chamber site. Additionally, quadruplicates of PRS probes were inserted at hummocks and hollows within each site.

Chapter 3

The Effects of a Semi-permanent Road on Spatio-Temporal Nutrient and CO$_2$ Dynamics in a Poor fen in the Western Boreal Plain

Introduction

Peatlands are important ecosystems for controlling the global carbon and nitrogen budgets (Wray and Bayley, 2007; Loisel *et al.,* 2014) and have been estimated to sequester 30% of the world's total soil carbon (Gorham, 1991). In the Western Boreal Plains (WBP) of Alberta, Canada, 20 to 50% of the terrain is covered by peatlands (Vitt *et al.*, 1995). However, this region is under pressure from industrial disturbance such as oil and gas extraction and road construction. It is largely unclear how disturbance may impact peatland ecosystem health and biogeochemical function. An improved understanding of biogeochemical processes in this landscape and how they respond to disturbance may assist us in predicting the overall impacts of industrial pressure on peatland ecosystem health. If critical thresholds on nutrient biogeochemical processes are characterized than these can act as guidelines on how the key drivers of these processes should be managed in reclamation practices.

Most previous work on biogeochemical processes in peatlands has evaluated the effects of climate variability or drainage (Holden, 2004; Macrae *et al.*, 2013; Mettrop, *et al.*, 2014). Little is known about the impacts of surface disturbances (road construction) on biogeochemical processes in peatlands. Roads have the potential to impede drainage within peatlands if placed perpendicular to the direction of groundwater movement,

modifying peatland hydrologic conditions by enhancing drying in some sections of a peatland and flooding others. This hydrologic variability has the potential to directly or indirectly impact the cycles of N, P and C in this landscape, and consequently ecosystem health.

The key drivers of nutrient dynamics within northern peatlands include water table depth, redox conditions, soil moisture, temperature, vegetation composition, and microbial communities and activity (Pastor *et al.*, 1984; Richardson and Marshall, 1989; Updegraff *et al.*, 1995; Jonasson and Shaver, 1999; Keller *et al.,* 2004; Wray and Bayley, 2008). However, the dominant drivers on nitrogen (N) and phosphorus (P) exchange processes may differ, and appear to vary across different studies in different peatlands (Pastor *et al.*, 1984; Updegraff *et al.*, 1995; Kellogg *et al.*, 2003; Keller *et al.*, 2004; Mack *et al.*, 2004; Chen *et al.*, 2012). Similarly, CO_2 uptake and release rates have been linked to interrelationships among similar abiotic factors (e.g. hydrology, precipitation, groundwater supply, evapotranspiration rates, PAR, plant communities and structure and diversity within a peatland (Szumigalski and Bayley, 1997; Chivers *et al.*, 2009; Szumigalski and Bayley, 1997; Alm *et al.*, 1999; Blodau, 2002; Chivers *et al.*, 2009; Webster *et al.*, 2013; Waddington and Roulet, 2000; Gorham, 1991; Bubier et al., 1998; Waddington et al., 1998; Griff *et al.*, 2000). As has been shown for nutrient dynamics, the dominant drivers of CO_2 exchange processes appear to vary spatially across different peatland studies.

Given the complex and highly spatially variable controls on nutrient and CO_2 exchange that have been reported, it is unclear if hydrologic variability in the WBP caused by disturbance will affect N, P and C dynamics, and if these cycles will be affected in the same way and to the same extent. The effects of disturbance on one or more of these

cycles may subsequently impact another cycle as complex couplings exist among vegetation productivity, N and P availability, maintained by feedback loops involving nutrient mineralization, plant uptake of nutrients and the return of nutrients to a system via litterfall (Pastor *et al.*, 1984) such interactions may ultimately impact ecosystem health and resiliency. Previous studies have reported positive correlations between above ground productivity on N retention (Updegraff *et al.*, 2001) and N mineralization (Pastor *et al.*, 1984). Aerts *et al.* (1995), which suggest that apparent linkages between N, P and CO_2 would be dependent on whether a peatland is N or P limited. However, these studies are limited in number and extensive research on whether these relationships exist in peatlands in the WBP remains to be seen. Peatlands are complex systems and the ability to differentiate direct relationships between controls of C (e.g. nutrients) and CO_2 dynamics have been difficult to achieve in field studies (Aerts and Ludwig, 1997; Blodau, 2002 and Knorr *et al.*, 2009).

The objectives of this study are (1) to examine spatiotemporal variability in nitrogen and phosphorus dynamics (nutrient pools, supply rates and mineralization rates) and CO_2 dynamics (net ecosystem exchange, respiration and gross ecosystem production), (2) to determine if relationships exist between nutrient and CO_2 dynamics and their environmental controls, and (3) to determine the effects of a linear disturbance (semi-permanent road) on nutrient and CO_2 dynamics.

Materials and Methods

Study Site

Research was conducted between May and September, 2012 on a poor fen located in the Athabasca oil sands (AOS) at Japan Canada Oil Sands Limited (JACOS), located 50 km south of Fort McMurray, Alberta, Canada (56^0 19' N, 111^0 39' W). In 2001, a semi-permanent road constructed of geotextile layers was developed across 450 m of the study site (Figure 3.1). The road bisected the site, running perpendicular to the natural flow of water, which flows south to northwest. As a result, the study site was divided into two main sections, the south side of the road (down stream) and the north side of the road (upstream). In 2011, three sections on the eastern part of the road were removed and re-vegetation plots were implanted in order to examine potential for site reclamation.

The upper 10 cm peat layer had similar physical characteristics between the two sides of the road (Table 3.1). Peat quality did not differ between the two sides of the road, but C:N ratios in hummocks were greater than in hollows (Table 3.1). Vegetation communities were comprised of *Sphagnum* moss cover and few vascular plant species such as *Groenlandicum* (Labrador tea) and *Vaccinium vitis-idaea* (large bog cranberry). The south side of the road had more moss (*Sphagnum*) biomass than the north side, and, the north side hosted vegetation species that were not located on the south side, including *Polytrichum spp.* and different *Cladonia spp.* (Table 3.2). Above ground vascular biomass was comparable across both sides of the road (262-1204 g m^{-2}). The density of *Sphagnum* moss did not differ between hummocks and hollows; however, hummocks had greater above ground vascular plant biomass than hollows (Table 3.2).

Methods

Sampling Design

Six study plots were located on both sides of the road (N = 12 plots). Of the six plots on

each side of the road, three plots were located parallel to the reclaimed area of the road

and three plots were located parallel to the intact road (Figure 3.1). Each plot had two

semi-permanent collars for chamber measurements of CO_2 exchange (one in a hummock

and one in a hollow), one 5 cm (ID) PVC well (1 m depth) situated at the midpoint

between a hummock and hollow, and a 5x25 cm boardwalk to limit compaction of peat

while collecting samples. Nutrient and CO_2 dynamics were examined at each of these

plots between May to August, 2012.

Table 3.1: Soil properties of the south and north side of the study site[a]

Side of Road	Soil Depth (cm)	Specific Yield	Bulk Density $(g\ cm^{-3})$	Porosity (Φ)	Organic Content (%)	C:N[b]
South Hummocks (wet)	0-5	0.20 ± 0.06	0.01 ± 0.01	0.99 ± 0	98	88
	5-10	0.19 ± 0.04	0.02 ± 0.01	0.99 ± 0		
	10-20	0.14 ± 0.02	0.05 ± 0.02	0.96 ± 0.01		
	20-30	0.16 ± 0.03	0.04 ± 0.02	0.97 ± 0.01		
South Hollows (wet)	0-5	0.27 ± 0.04	0.01 ± 0.01	0.99 ± 0	96	63
	5-10	0.18 ± 0.03	0.03 ± 0.01	0.98 ± 0.01		
	10-20	0.13 ±0.03	0.08 ± 0.04	0.94 ± 0.02		
	20-30	0.16 ± 0.01	0.03 ± 0.02	0.98 ± 0.02		
North Hummocks (dry)	0-5	0.32 ± 0.14	0.01 ± 0	0.99 ± 0	99	83
	5-10	0.17 ± 0.03	0.02 ± 0.02	0.99 ± 0		
	10-20	0.18 ± 0.03	0.06 ± 0.02	0.96 ± 0.01		
	20-30	0.16 ± 0.03	0.06 ± 0.03	0.96 ± 0.01		
North Hollows (dry)	0-5	0.25 ± 0.09	0.03 ± 0.02	0.98 ± 0.02	96	51
	5-10	0.19 ± 0.06	0.09 ± 0.03	0.94 ± 0.02		
	10-20	0.11 ± 0.03	0.14 ± 0.06	0.90 ± 0.04		
	20-30	0.09 ± 0.02	0.15 ± 0.09	0.90 ± 0.06		

[a]Values are averaged (n = 4) with *SD*.
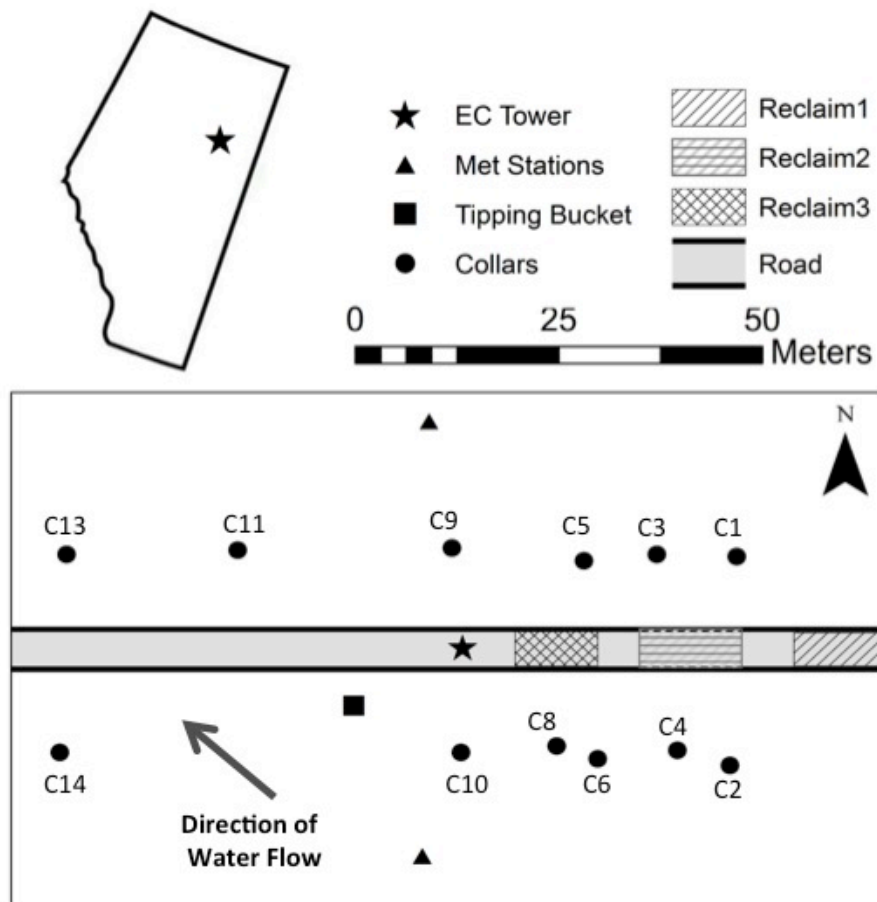
Figure 3.1: JACOS fen study site. The circles show the 12 chamber plots used in the current study. The arrow on the bottom left of the figure provides the direction of surface and groundwater flow. The south side of the fen was found to be the wet side, whereas the north side was relatively dry. The rectangles located on the eastern side of the road represent the reclamation sites.

Table 3.2: Total belowground and aboveground biomass, dominant and codominant vegetation, total LAI and species LAI at each chamber site[ab]

Chamber Site	Vegetation Species	*Total BG Biomass (g m^{-2})	*Total AG Biomass (g m^{-2})	AG Biomass (%)	*Total LAI (m^{-2} m^{-2})	Species LAI (m^{-2} m^{-2})
1 Hummock	*Rhododendron groenlandicum*	353	835	50	1.7	0.3
	Spagnum sp.			36		1.0
	Vaccinium vitis-idaea			10		0.2
1 Hollow	*Carex sp.*	443	317	43	2.0	0.6
	Sphagnum sp.			25		0.3
	Rubus chamaemorus			18		0.3
	Vaccinium vitis-idaea			9		0.1
2 Hummock	*Vaccinium vitis-idaea*	768	770	51	1.7	0.6
	Sphagnum fuscum			38		0.8
	Rhododendron groenlandicum			4		9.0 x 10^{-3}
2 Hollow	*Sphagnum fuscum*	168	384	95	1.5	1.5
3 Hummock	*Polytrichum sp.*	1237	833	50	1.5	0.7
	Rhododendron groenlandicum			22		0.2
	Chamaedaphne calyculata			15		9.0 x 10^{-2}
	Vaccinium vitis-idaea			7		0.2
3 Hollow	*Rhododendron groenlandicum*	516	1204	56	2.6	0.4
	Sphagnum sp.			43		2.2
4 Hummock	*Sphagnum fuscum*	271	910	76	4.3	3.5
	Vaccinium vitis-idaea			15		0.5
	Rhododendron groenlandicum			4		6.0 x 10^{-2}
4 Hollow	*Sphagnum sp.*	247	536	79	3.4	3.1
	Rhododendron groenlandicum			20		0.2
5 Hummock	*Sphagnum fuscum*	515	798	67	2.5	2.0
	Vaccinium vitis-idaea			16		0.3
	Rhododendron groenlandicum			15		0.1
5 Hollow	*Cladonia sp.*	267	472	63	1.0	0.6
	Cladina stellaris			26		0.3
	Polytrichum sp.			7		9.88 x 10^{-4}
6 Hummock	*Sphagnum fuscum*	212	631	70	2.6	2.2
	Rhododendron groenlandicum			23		0.2
	Vaccinium vitis-idaea			2		4.7 x 10^{-2}
6 Hollow	*Sphagnum sp.*	1011	642	98	1.8	1.6
8 Hummock	*Sphagnum fuscum*	301	543	86	2.3	2.0
	Vaccinium vitis-idaea			9		0.1
	Rhododendron groenlandicum			1		1.4 x 10^{-2}
8 Hollow	*Sphagnum sp.*	629	494	64	3.7	3.1
	Chamaedaphne calyculata			25		0.3
	Vaccinium vitis-idaea			5		0.1
9 Hummock	*Rhododendron groenlandicum*	949	581	88	1.0	0.6
	Vaccinium vitis-idaea			9		0.3
9 Hollow	*Polytrichum sp.*	190	414	71	1.5	1.1
	Cladonia sp.			15		0.2
	Rhododendron groenlandicum			7		9.2 x 10^{-2}
10 Hummock	*Sphagnum fuscum*	270	1192	87	2.7	2.4
	Vaccinium vitis-idaea			8		0.2
	Rhododendron groenlandicum			5		3.2 x 10^{-2}
10 Hollow	*Sphagnum sp.*	340	545	94	1.7	1.7
	Rhododendron groenlandicum			5		7.9 x 10^{-3}
	Vaccinium vitis-idaea			1		7.4 x 10^{-3}
11 Hummock	*Sphagnum fuscum*	632	534	65	1.6	1.3
	Rhododendron groenlandicum			17		4.4 x 10^{-2}
	Vaccinium vitis-idaea			15		0.2
11 Hollow	*Polytrichum sp.*	147	380	81	1.0	0.8
	Vaccinium vitis-idaea			8		6.6 x 10^{-2}
	Rhododendron groenlandicum			3		1.2 x 10^{-3}
13 Hummock	*Sphagnum fuscum*	566	306	24	7.9	0.2
	Rhododendron groenlandicum			35		0.2
	Vaccinium vitis-idaea			22		0.2
	Cladina Stellaris			12		0.2
13 Hollow	*Polytrichum sp.*	265	262	63	0.9	0.6
	Rhododendron groenlandicum			26		0.1
14 Hummock	*Sphagnum fuscum*	666	654	57	2.7	1.7
	Rhododendron groenlandicum			33		0.7
	Vaccinium vitis-idaea			5		0.1
14 Hollow	*Sphagnum fuscum*	129	527	87	3.2	3.0
	Picea mariana			8		0.2
	Vaccinium vitis-idaea			3		7.20x 10^{-2}
	Rhododendron groenlandicum			2		2.6x 10^{-2}

[a] Dominant and codomiant non-vasuclar species include *Sphganum fuscum* and *Sphagnum* spp. (Sphagnum moss), *Polytrichum sp.* (hair moss), *Cladina stellaris* (reindeer lichen) and *Clandonia sp.* (cup lichen). Dominant and codominant vascular species include

Vaccinium vitis-idaea (large bog cranberry), *Rhododendron groenlandicum* (Labrador tea), *Chamaedaphne calyculata* (leather leaf), *Rubus chamaemorus* (cloud berry) *Carex sp.* (sedge or shrub) and *Picea mariana* (black spruce).
[b] Chamber sites having an even number are located on the south side of the site whereas, odd chamber sites are located on the north side.
* Total below ground, above ground biomass and total leaf area index (LAI) is the sum of every vegetation species within each chamber.

Nutrient Dynamics

To determine extractable N and P nutrient pools and net mineralization rates paired peat cores were collected at a hummock and hollow of each study plot (n = 6 hummocks and 6 hollows on each site of road). The first core was taken back to the lab for processing and the second core was placed in a polyethylene bag to exclude vegetation roots and leaching and incubated in the hole from which it was collected (after Eno, 1960) for a period of three weeks, at which point it was retrieved and processed. The paired cores were compared at the end of the study in Waterloo, ON. This was done three times between May 28 and August 7, 2012, creating three periods Period 1 (JD 149-172), Period 2 (JD 172-194) and Period 3 (JD 198-220). Additional cores were collected in September 15, 2012 to provide an estimate of nutrient pools at the end of the growing season. Peat cores were collected with a galvanized duct pipe (10 x 10 x 10 cm deep) and a serrated knife to minimize the compaction of peat and were placed in polyethylene bags. To prevent oxygen from affecting the cores collected in anoxic conditions, all excess air was removed from these bags and sealed. Cores were kept in a cooler with ice until processed (within 12 to 24 hours of collection). To ensure the samples were representative of the study site, samples were mixed by hand while still in the original bags until homogenized. Sub-samples (~10 g) were shaken for one hour in 50 ml of de-mineralized water for water extractable P (WEP) and 2M KCl for nitrate (NO_3^-) and ammonium (NH_4^+) pools (after Binkley and Hart, 1989) and immediately gravity filtered through Whatman 42 ashless filter paper and frozen.

WEP, NO_3^- and NH_4^+ were determined colorimetrically in the Biogeochemistry Lab at the University of Waterloo (Bran Luebbe AA3, Seal Analytical, Seattle, U.S.A., Methods G-102-93 (NH_4^-), G-109-94 ($NO_3^-+NO_2^-$), G-103-93 (SRP)) and are presented throughout this paper in microgram per gram of dry weight of peat (µg/g). Net nitrification and net N and P mineralization rates were estimated by subtracting the nutrient concentrations extracted from incubated (buried) bag from those from the initial core.

The remainder of peat samples collected for extractable nutrients and net nutrient transformation rates were stored in a freezer until further analyses on gravimetric soil moisture could be determined at the University of Waterloo, ON. Unfortunately, some of the residual peat samples were lost during the transition from Fort McMurray, Alta. to Waterloo, ON. In order to estimate the gravimetric soil moisture of these bags, to permit the expression of extractable nutrients per unit *dry* weight of peat soil, a relationship and fitted curve between known gravimetric soil moisture conditions and the corresponding field moisture measurements (determined by a Hydro-sense probe; Campbell Scientific, Canada and a theta moisture probe; Delta T Devices, England) was used. Organic content (LOI), bulk density and porosity were determined (using standard methods) on sub samples of the peat cores collected for extractable nutrient pools. Total carbon and total nitrogen ratios were determined on peat samples collected in September using Thermo Finnigan-Delta plus elemental analyzer-isotope ratio mass spectrometer (EA-IRMS) at the Environmental Isotope Laboratory, Dept. of Earth Sciences, University of Waterloo, ON.

To estimate the availability and supply of P and N in peat, plant root simulator probes (PRS probes; Western Ag. Innovations, Canada) were placed 10 cm below the peat surface and kept in place during the same time intervals as the buried bag incubations. At

the end of each incubation period, the probes were gently removed from the peat, placed in polyethylene bags and all remaining soil was removed using demineralized water within 24 to 72 hours of removal. Once cleaned, the probes were placed in new polyethylene bags, which were stored in a cool, dry location until shipped to Western Ag Innovations for the analyses of major cations (NH_4^+ Ca^{2+}, Mg^{2+} and K^+), anions, micronutrients and metals (NO_3^-, $H_2PO_4^-$, SO_4^{2-}, Fe, Mn, Al, Cu, Zn, B, Cd and Pb). Nutrient supply rates are expressed in units of mass/unit length of probe/ burial length and therefore cannot be directly compared to mineralization rates or pools of nutrients in peat, although spatiotemporal patterns in each of these can be related.

Shallow groundwater samples were collected from wells (purged 24-72 hrs prior) twice per week over the study period (on same date as CO2 measurements taken). Subsamples were filtered (0.45 μm) in the field using a hand pump and flipmate filtration systems (Delta Scientific Laboratory Products Inc., Canada) and frozen until analyses for soluble reactive P (SRP), NO_3^- and NH_4^+. An additional subsample was acidified (to 0.2% H_2SO_4) and stored for the analyses of Kjeldahl nitrogen and phosphorus. Samples were analyzed in the Biogeochemistry Lab at the University of Waterloo (Bran Luebbe AA3, Seal Analytical, Seattle, U.S.A., Methods G-189-097 (TKN), G-188-097 (TP)).

Carbon Dioxide Measurements

Instantaneous measurements of net exchange of CO_2 between the peat surface and the atmosphere were measured at a hummock and hollow of each study plot using an EGM-4 Infrared Gas Analyzer (IRGA) (P.P. Systems, Maryland, USA). Measurements of gross ecosystem productivity (GEP), total respiration (R_{tot}) and net ecosystem exchange (NEE)

were conducted between late May to late August 2012. Clear lexan chambers (12 560 cm^3) were used to measure GEP and NEE; chambers were covered with an opaque neoprene shroud to measure respiration rates (Figure 5). The chambers were placed into the grooves of polyvinylchloride (PVC) collars (4 534 cm^3) that were inserted at each site (to a depth of 20 cm). To ensure the chamber and collar formed an airtight seal, the groove of the collar was filled with water prior to the placement of the chamber and remained sealed throughout the measurement. Chambers consisted of an internal fan to regulate the gradient by limiting CO_2 concentration buildup (Welles *et al.*, 2001) and chambers were aired out in between measurements. Internal temperature was controlled with a cooling system, where cold water could be pumped through a coolant tube to keep chamber temperatures within 5^{0}C from the atmosphere. Measurements were recorded twice a week between 9 to 1900 hours and to ensure that the sites received varying hours of sunlight the time of measurements for each site were selected randomly. Each measurement consisted of five, 1-minute intervals and an average of the rate of CO_2 concentration over this interval was used to determine the flux for that given sample (Lund *et al.*, 1999). The following equation was used to determine the flux of R_{tot} and NEE:

$$F = \frac{\Delta \ MM}{N} \times \frac{V}{A} \times CF \tag{8}$$

Where, F is the gas flux (gCO$_2$ m^{-2} d^{-1}), Δ is the linear change in CO_2 over the 5 minute interval (ppm sec^{-1}), MM represents the molar mass of CO_2 (44.01 g mol^{-1}), N is the molar volume of a gas at standard temperature and pressure (22.414 L mol^{-1}), V is the corrected volume of the chamber (m^3), A is the area of the chamber (m^2) and CF is the conversion factor from ppm to mol (1ppm is equivalent to 10^{-6} mol). An adjustment measurement of

vegetation growth within the collar was taken every two weeks to correct for the chamber volume.

GEP was determined by subtracting R_{tot} from NEE. Samples were collected twice per week, and then grouped into three periods; JD 149-172, 172-194 and 198-220 which corresponded with nutrient incubation periods. Carbon uptake throughout this study is represented by negative values, whereas CO_2 release is shown with negative values.

Environmental Variables

Ambient temperature, peat temperature, soil moisture and relative humidity (RH) were recorded daily at 30 minute intervals from May to September, 2012 using two micrometeorological stations (CR10x, Campbell Scientific, Canada) set up on the south and north side of the study site. Both stations had connections to RH and ambient temperature probes (Onset, USA), T copper constantan thermocouples measured ground temperatures at 2, 5, 10, 25 and 50 cm depths and TDRs to measure soil moisture at a 0-25 cm depth (Cs616 TDR, Campbell Scientific, Canada). Daily precipitation was recorded with a tipping bucket rain gauge (Rg3-M, Onset, USA) located in an open area on the south side of the site.

Manual measurements of peat temperature, soil moisture and water table position (relative to peat surface), depth to anoxia (redox) and depth to ice were recorded at both microforms at each plot with nutrient extractions (once every three weeks) and CO_2 flux measurements (twice a week). A thermistor probe (Omega, Canada) was used to determine soil temperature at depths of 2, 5 and 10 cm below the surface. Soil moisture was recorded with either a Hydro-sense probe (Campbell Scientific, Canada) or a theta

soil moisture probe (Delta-T devices, England). The probes were inserted vertically into the soil adjacent to the peat cores collected for nutrient extractions, PRS probes and chamber plots. Peat cores were extracted in September, 2012 and transported to the University of Waterloo, where they were used to determine a calibration curve with fitted data for both probes. Raw field data was corrected based on the equations determined by the calibration curve for the given probe.

PVC wells were used to measure water table depth and collect groundwater nutrient samples at each chamber plot twice a week corresponding with CO_2 measurements. It should be noted, that water table positions were determined before the collection of water samples.

Redox conditions at each site were estimated by two different methods. In the first method, thin iron rods were inserted at a hummock and hollow at each plot to a depth of approximately 55 cm (over the first month of the study the depth of the wire was dependent on the depth of ice). Redox conditions at the site (relative to the peat surface) were inferred using visual clues on the iron rods. Aerobic conditions were indicated by the presence of rust. Suboxic and anoxic conditions were assumed to be present based on black and silver colorings on the metal wire, respectively. Redox conditions at each plot were also inferred using data collected using the PRS probes and briefly, concentrations of Fe and Mn were used to provide clues regarding prevalent redox conditions across the sites.

Depth to ice was measured at a hummock and hollow of each site using a metal rod (1 m in length). The rod was inserted vertically until resistance from a layer of ice was felt

and that depth was recorded relative to the peat surface. Measurements were collected until ice was below 1 m depth (June).

Photosynthetically active radiation (PAR), internal ambient chamber temperature and external soil temperature were measured at each chamber plot over the 5-minute interval of CO_2 sampling. PAR and internal chamber temperatures were determined using an IRGA (P.P. Systems, Maryland, USA) and external soil temperatures of peat within 5 cm from the chamber were measured at 2, 5 and 10 cm depths with a digital thermometer.

Vegetation Analyses

In September 2012, after the study had been completed, the contents (peat and vegetation) of each collar were removed using a serrated knife (to minimize compaction of peat). To preserve the integrity of the sample, the below ground section of the collars' cores were wrapped in polyethelene wrap and the intact core was stored in a large paper bag in a cool dry location until analyses could be completed at the University of Waterloo, ON.

Aboveground biomass was estimated for each chamber by removing all vegetation (vascular and non-vascular) above the peat surface. The dried foliar mass was determined by removing and arranging the stems and leaves by species, microform and plot and dried at 80^oC for 24 hours. Estimated biomass for each vascular species was then calculated using

$$\text{Aboveground biomass} = \frac{\text{dry mass (g)}}{A \text{ (m)}} \qquad (9)$$

Dry mass is the dry mass of the leaves and stems of an individual vascular species or the upper layer of non-vascular species and A is the area of the collar. Before foliar biomass were dried, the wet biomass of leaves and non-vascular plants were separated by species

and collar plot. LAI was estimated using a LI-3100C Area Meter (LI-COR Inc., Lincoln, Nebraska, USA). The estimated LAI was given in mm^2; this was then converted to $m^2\ m^{-2}$ by converting mm^2 to m^2 (1 mm^2 is equivalent to $10^{-6}\ m^2$) and then dividing by the area of the collar (m^2).

To estimate the belowground biomass of each collar, the roots were removed and dried at $80^{o}C$ for 24 hours. The roots were not separated by species and instead the total belowground biomass for each collar was determined:

$$\text{Belowground biomass} = \frac{\text{total dry mass (g)}}{A\ (m)} \tag{10}$$

Where, total dry mass is the total mass of all roots in a sample and A is the area of the collar.

Statistical Analyses

Seasonal variations in nutrient and CO_2 dynamics were determined by grouping data into respective incubation periods. Nutrient pools, nutrient groundwater content, net transformation rates and P supply rates did not pass the assumptions for parametric tests, therefore Kruskal Wallis tests were used to determine if seasonal variation existed and Mann-Whitney U tests directly compared nutrient dynamics between two incubation periods. An alpha correction was applied (Bonferroni, $\alpha = 0.017$). To determine spatial variations, non-parametric tests were used to compare differences between the two microforms (hummocks and hollows).

N (NO_3^- + TIN) supply rates were transformed using log + 1 and passed assumptions for a 2-way analysis of variance (ANOVA). A post hoc test (tukey) was

applied to each 2-way ANOVA and microform and incubation period were the fixed factors.

2x2 Repeated measures ANOVAs were used to determine spatial and temporal variations in CO_2 dynamics. CO_2 flux rates (GEP, R_{tot}, and NEE) of each plot (n = 12) were averaged over each incubation period (n =3) and used as the dependent variable. Incubation period and microform were the within-subject factors.

Spearman correlations and regressions were used to examine the effects of N on CO_2 exchange. For each of these tests, N dynamics and median CO_2 flux rates from corresponding chamber plots were compared (data was not divided by incubation period).

Mann- Whitney U tests were used To determine the effects of the road on N pools, groundwater N and Net N transformation rates. Each Mann-Whitney U test compared the north and south side of the road. Data was split by incubation periods to see if the effects of the road varied throughout the season. To determine the effects of the road on N supply rates, three 2-way ANOVAs with microform and side of road as independent factors were used. Each ANOVA represented a different incubation period and a Bonferroni alpha correction was applied.

A general linear model was used to determine the impact of the semi-permanent road on CO_2 dynamics. The side of road and type of microform were independent variables and the incubation period was the random factor.

Regressions as well as Spearman's correlation tests were used to determine relationships between N and CO_2. Interaction terms and plots were examined in all parametric analyses, however no significant interaction effects were found. Analyses were all performed using IBM SPSS software (v. 21).

Results

Climatic and Environmental Conditions throughout the Study Period

The study season had dry conditions in June and August (40 mm and 18 mm, compared to long-term 30 year mean (*M*) of 74.8 mm and 72.2 mm, respectively) but wet and warm conditions in July (134 mm and 19.8 C, compared to long-term means of 81.3 mm and 16.8 C). Thus, Incubation Period 1 (May 28-June 20) was cool and dry, Incubation Period 2 (June 20-July 12) was hot and wet, and Incubation Period 3 (July 16-August 7) was warm and moist (Figure 3.2).

   Hollows were wetter than hummocks (U = 2987, p < 0.001), having a VWC between 50 to 43%, where water content in hummocks fell between 33 to 28%. Peat surface temperatures did not vary spatially and depth to anoxic conditions were comparable across all three periods (U, p > 0.05, Table 3.3). Data collected using PRS probes and metal (iron) wire to infer the presence of reducing conditions suggests that both hummocks and hollows (0-20cm) were generally oxic throughout most of the study period (Table 3.3). However, elevated concentrations of Fe and Mn (> 20 mg/m^2/incubation; found using PRS probes) were present in a subset (~ 50%) of hollows during Periods 2 and 3 suggesting that these hollows were anoxic and acidic from late June through August (Western Ag. Inc., 2014).

Table 3.3: Comparison of redox via depth to anoxia (cm below peat surface) and by iron (Fe, mg/m^2/3weeks) and manganese (Mn, mg/m^2/3weeks) soil concentrations. All measurements were recorded in hummocks and hollows throughtout each incubation period.[a]

Incubation Period	Microform	Depth to anoxia (cm below peat surface ± SD) [b]	Fe (mg/m^2/3week ±SD)[c]	Mn (mg/m^2/3weeks ± SD)[c]
1	Hummock	21 ± 13	3.5 ± 1.7	7.4 ± 7.9
	Hollow	14 ± 6	4.7 ± 4.6	9.5 ± 8.3
2	Hummock	20 ± 11	3.3 ± 0.2	8.8 ± 4.9
	Hollow	7 ± 9	5.0 ± 26.4	13.5 ± 20.3
3	Hummock	22 ± 11	1.3 ± 1.5	5.8 ± 3.7
	Hollow	7 ± 9	10.4 ± 53.3	13.2 ± 20.0

[a] All values shown in median values with standard deviation
[b] Depth to anoxia was determined by metal wire of iron survey flags, conditions were deemed anoxic when the wire changed from rust to silver.
[c] Concentrations 10cm below the peat surface, as determined by PRS probes.

Temporal and Spatial Trends in Nitrogen Dynamics

Peat N content and transformation rates varied seasonally. Ext- NO_3^- and ext-TIN (NO_3^- + NH_4^+) increased from Period 1 through Period 3 (Figure 3.3, $H(2) = 50.48$, $p < 0.001$ and $H(2) = 34.75$, $p < 0.001$, respectively), but did not appear to vary between microforms for NO_3^- ($H(1) = 0.508$, $p = 0.476$) or TIN ($H(1) = 0.425$ $p = 0.514$) (Figure 3.3a) although hollows were more spatially variable than hummocks. Nitrogen net transformation rates (mineralization and nitrification) did not increase throughout the season and were instead greater during Incubation 2 than during the other two periods (U, p values < 0.001). Transformation rates did not differ between microforms ($H(1) = 0.004$, $p = 0.948$ N mineralization; $H(1) = 0.212$, $p = 0.645$ nitrification). During Incubation 1, N transformation rates were close to zero, suggesting that gross mineralization rates were low, or, mineralization rates were closely matched by immobilization. During Incubation
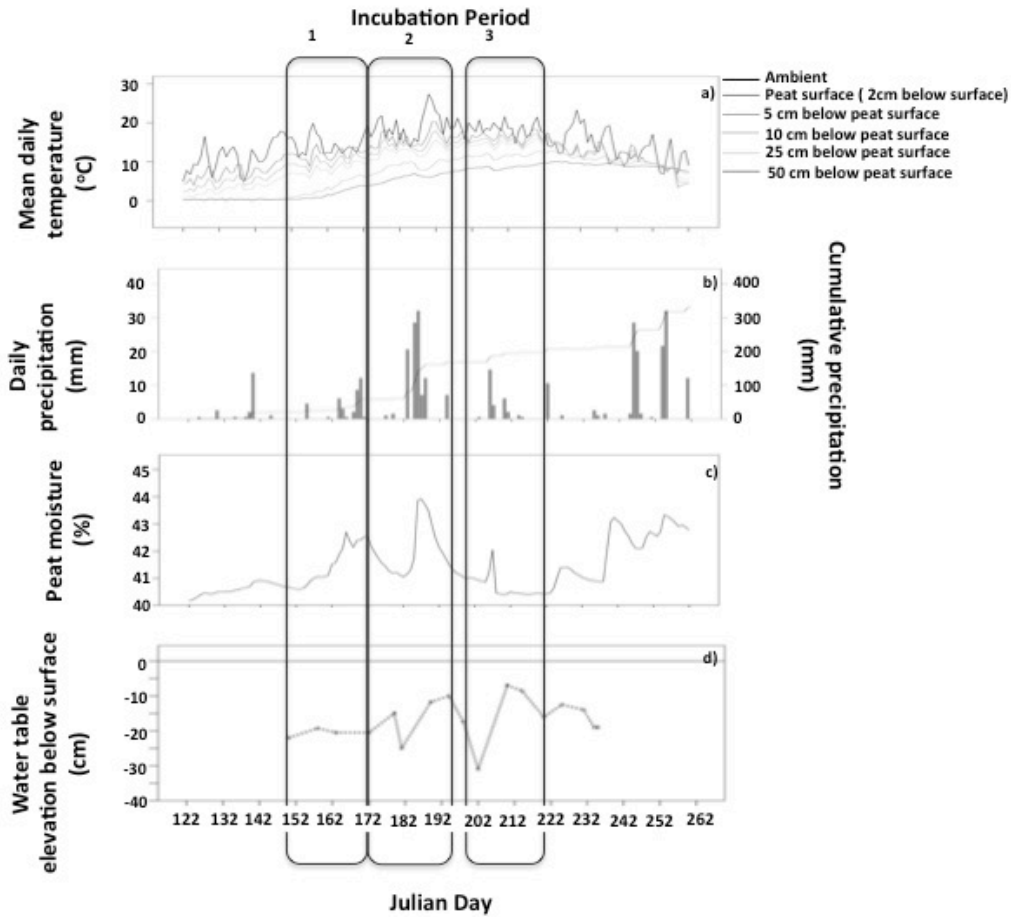
Figure 3.2: Comparison of climatic and environmental variables throughout the season. (a) ambient and soil temperature, (b) daily and cumulative precipitation, (c) volumetric soil moisture and (d) median water table depth (using 12 sampling points on each date). The three incubation periods are highlighted in the figure.

3, which followed the peak period of N mineralization, N transformations were dominated by immobilization (Figure 3.3b). Observed changes in extractable nutrient pools exceeded net N transformation rates in incubated samples over the same period, suggesting that an external supply of N was present. Seasonal trends in N supply rates as determined by PRS probes were similar to ext-N pools, with greatest N supply rates over Period 3 (July to August, Figure 3.3). It is important to note that nutrient pools represent peat extractable nutrients at the *beginning* of the incubation period whereas nutrient mineralization rates and supply rates are data integrated across the entire three-week period. As such, these are not directly comparable because they do not correspond with the same time periods. A two-way ANOVA with a post-hoc test (Tukey) indicated that the supplies of TIN and NO_3^- were significantly higher in Period 3 than the other two periods (p values < 0.001). Total inorganic N supply was greater in hollows than hummocks ($F (1, 66)$, $p < 0.001$), but differences in NO_3^- supply between microforms were not significant.

Groundwater N was also variable throughout the season (Figure 3.4), with larger TIN and NO_3^- concentrations observed during Period 1 (median (*Mdn*) 0.344 mg TIN/L and 0.013 mg NO_3 -N/L) and Period 3 (*Mdn* 0.213 mg TIN/L and 0.007 mg NO_3-N/L) relative to Period 2. In general, N concentrations in shallow groundwater declined during and following precipitation events (Figure 3.4).

N transformation rates were driven by temperature rather than moisture conditions. Net mineralization rates and net nitrification rates positively correlated with both peat temperature at the surface (net N mineralization $r_s (68) = 0.427$, $p < 0.001$; net nitrification $r_s (68) = 0.715$, $p<0.001$) and 10 cm depth (net N mineralization $r_s (68) = 0.423$, $p < 0.001$; net nitrification $r_s (68) = 0.612$, $p < 0.001$). Net N mineralization and nitrification rates

were not significantly correlated with peat moisture or water table position. Surface temperatures had an effect on TIN supply rates (r_s (68) = -0.353, p = 0.003) and NO_3^- supply rates (PRS probes) were negatively correlated with temperatures at the surface (r_s (68) = -0.504, p < 0.001) and 10 cm (r_s (68) = -0.297, p = 0.013). Water table position had no impact on both TIN and NO_3^- supply rates (r_s (68) = -0.181, p = 0.133 and r_s (68) = 0.298, p = 0.012 and) but peat VWC had an effect on TIN supply (r_s (68) = 0.387, p = 0.001).

Temporal and Spatial Trends in Phosphorus Dynamics

Spatio-temporal trends in P were not consistent throughout the season. WEP pools were significantly higher in hollows than hummocks (H(1) = 15.896, p < 0.001). A significant seasonal trend was not found (H(2) = 0.839, p = 0.657, Figure 3.5a) despite the increase in pools within hollows in Period 3 (*Mdn* WEP ranged from 45 to 20 µg/g, Figure 3.5). Spatial variation was observed in net P mineralization rates, where mineralization was slightly higher in hummocks than hollows (H(1) = 4.659, p = 0.031) (Figure 3.5). No significant seasonal trends were determined in net P mineralization rates (H(2) = 5.592, p = 0.061, Figure 3.5b). P supply rates also varied spatially, where hollows had greater P supply rates than hummocks (H(1) = 11.075, p = 0.001, Figure 3.5c). However, unlike WEP and net P mineralization rates, P supply rates (determined by PRS probes) varied seasonally (H(2) = 14.761, p = 0.001, Figure 3.5c) with significantly higher supply rates during Period 1 (late May to late June) relative to Periods 2 and 3 (U = 125.000, p = 0.001 & U = 120.500, p = 0.002, respectively; Figure 3.5).
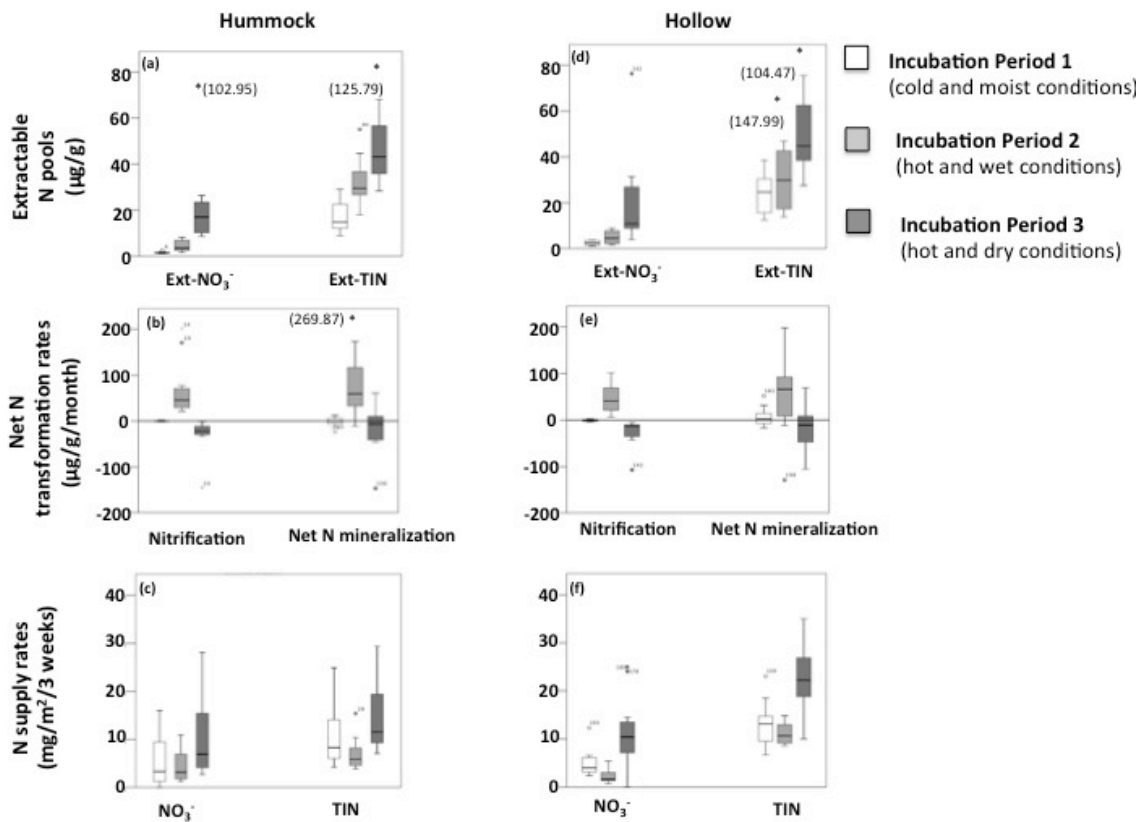
Figure 3.3: Box plots of seasonal and spatial variations in N dynamics. Nutrient dynamics include extractable nutrient pools (a and d), Net N transformation rates (b and e) and N availability in the soil after plant and microbial uptake (c and f). Forms of N are on the x-axis and temporal trends are characterized by the three incubation periods, where white boxes are period 1, light boxes represent period 2 and dark boxes indicate period 3. Microforms are separated, where hummocks are on the left (a,b and c) and hollows are on the right of the figure (d,e,f).
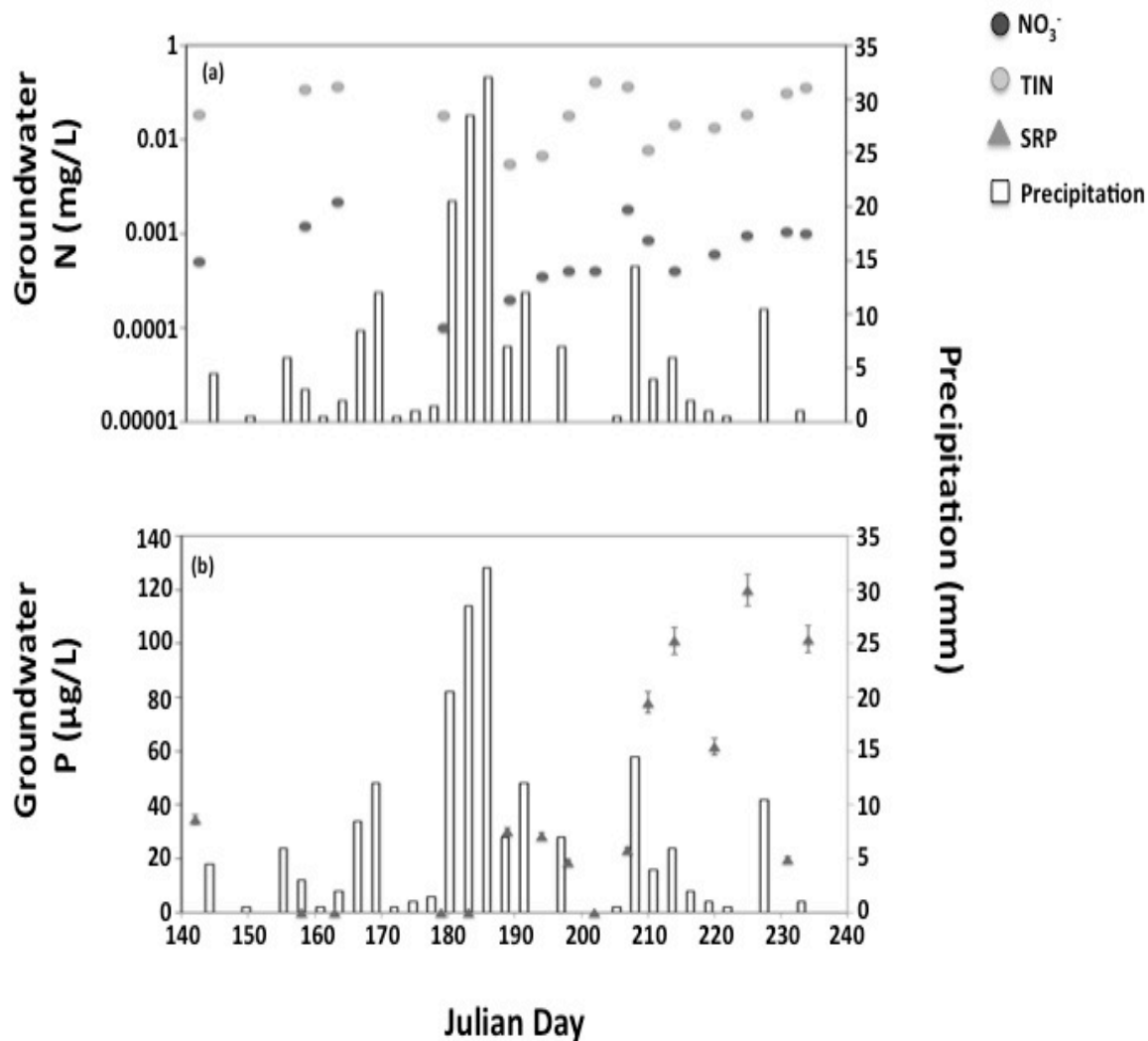
Figure 3.4: Daily precipitation with observed median N and P in groundwater throughout the season. Julian day of rain and sampling of groundwater is on the x-axis, median groundwater N is on the first y-axis on a logarithmic scale (a), where nitrate (NO_3^-) is shown as dark markers and total inorganic nitrogen (TIN) is shown as the light markers. Groundwater SRP is on the x-axis of (b) as triangles. Error bars represent a confidence limit of 95%. Daily precipitation is on the second y-axis of (a & b) as bars.

Soluble reactive P concentrations in groundwater were very small in Periods 1 and 2 (*Mdn* < µg 0.001 SRP/L, Figure 3.4), but substantially higher between mid July and August (Period 3), when *Mdn* SRP in groundwater was µg 45.75 SRP/L (Figure 3.4). This followed heavy rainfall that fell in July, but coincided largely with the Period (3) when temperatures were hot and hollows remained largely saturated and anoxic, suggesting that SRP was mobilized in hot, flooded conditions.

P dynamics seem to be driven more by water table position and not temperature. Net P mineralization rates were not affected by peat VWC (r_s (68) = -0.207, p = 0.086), water table position (r_s = -0.017, p = 0.890) or peat temperature (r_s(68) = 0.163 and 0.275, p values > 0.01; surface and 10 cm, respectively). In contrast, P supply rates (PRS probes) were negatively correlated with water table depth (r_s = -0.358, p = 0.020) but not with any of the other environmental variables measured.

Seasonal and Spatial Trends in Carbon Dioxide Flux Rates

Exchange rates of CO_2 increased gradually throughout the season for both CO_2 uptake (GEP) ($F(2,72)$ = 7.988, p = 0.008) and release (R_{tot}) ($F(2,72$ = 5.327, p = 0.029) (Figure 3.6). This was observed in both microforms; however, differences between microforms did not vary enough to be statistically different in rates of GEP, R_{tot} and NEE. The concurrent increases in CO_2 uptake and release throughout the season resulted in no differences in NEE seasonally (*F*(2, 72) = *1.162*, p = 0.335). The observed seasonal patterns in GEP and R_{tot} rates were significantly related to environmental conditions throughout the study period. For example, GEP was negatively correlated with PAR(*r* (195) = -0.329, p < 0.001) and peat surface temperature (*r* (195) = -0.369, p < 0.001,

Figure 3.7), which means productivity increased (become more negative) with these two variables. The total LAI of within individual chambers had a moderate, yet significant relationship with GEP (R^2 = 0.355; p = 0.002) (Figure 3.8). Relationships between GEP and RH or peat moisture were not found (r (195) = 0.008, p = 0.912 & r (178) = 0.042, p = 0.576) (Figure 3.7).

Respiration was positively related to peat temperature (R^2 = 0.097, p <0.001, Figure 3.9b) but not RH (p > 0.05) or soil moisture (p > 0.05). However, a moisture threshold was observed, where plots that had a moisture content below 45% VWC had greater R_{tot} rates and R_{tot} rates at 45% VWC and wetter were simply suppressed and did not increase or decrease with soil moisture content (Figure 3.9), as peats were likely anoxic (Table 3.3).

Relationships between N and CO$_2$

No relationships or correlations were found between CO_2 flux (GEP and R_{tot}) and N supply rates (PRS probes), N availability in peat (extractable N) or N in groundwater throughout the study season. For example, the amount of inorganic N in the peat did not influence the productivity of the site. This was observed throughout the season between GEP with ext-TIN (R^2 = 0.032; p = 0.415, R^2 = 0.097; p = 0.249 and R^2 0.074; p = 0.805; Periods 1, 2 and 3, respectively) and GEP with ext- NO_3^- (R^2 = 0.019, p = 0.688 (Period 1), R^2 = 0.002, p = 0.808 (Period2) and R^2 = 0.050, p = 0.975 (Period 3)).

No significant relationships were found between R_{tot} and net N mineralization (R^2 = 0.027, p = 0.504, R^2 = 0.038, p = 0.054 and R^2 = 0.154, p = 0.115) and the relationship

between R_{tot} and net nitrification were equally as weak ($R^2 = 0.074$, $p = 0.227$, $R^2 = 0.003$, $p = 0.080$, and $R^2 = 0.045$, $p = 0.547$ (Periods 1, 2 and 3, respectively).

No significant correlations between CO_2 and N were found between GEP and ext-TIN ($r_s (60) = -0.088$, $p = 0.494$), TIN supply rates ($r_s (62) = 0.096$, $p = 0.450$) and TIN in groundwater ($r_s (12) = 0.169$, $p = 0.563$, Figure 3.10), or between R_{tot} and net N mineralization rates ($r_s (65) = 0.205$, $p = 0.097$) or R_{tot} with TIN in groundwater ($r_s (12) = 0.475$, $p = 0.866$, Figure 3.10).

A significant interaction was found between groundwater N and incubation period, which could be why insignificant correlations were determined between GEP and groundwater N. This finding suggests the effects of groundwater N on GEP differed depending on incubation period. For example, an increase in groundwater N (TIN and NO_3^-) resulted in a slight increase in CO_2 uptake in Period 3, however, GEP rates were low with high N concentrations in Period 1 (Figure 3.10).
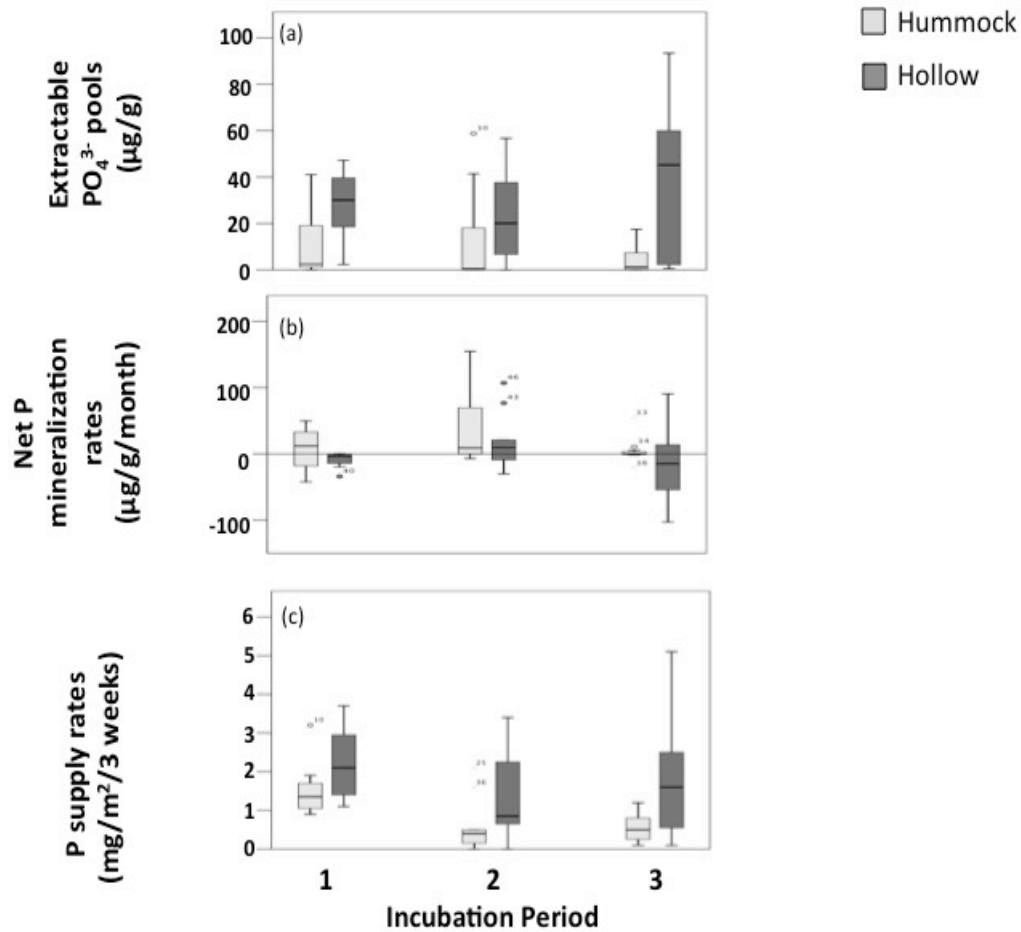
Figure 3.5: Box plots of temporal and spatial variations in P dynamics. The turn over of P is represented by extractable phosphate pools (a), Net P transformation rates (b) and P supply rates in peat after plant and microbial uptake (c). Incubation periods are on the x-axis. Hummocks (light boxes) and hollows (dark boxes) characterize spatial trends.
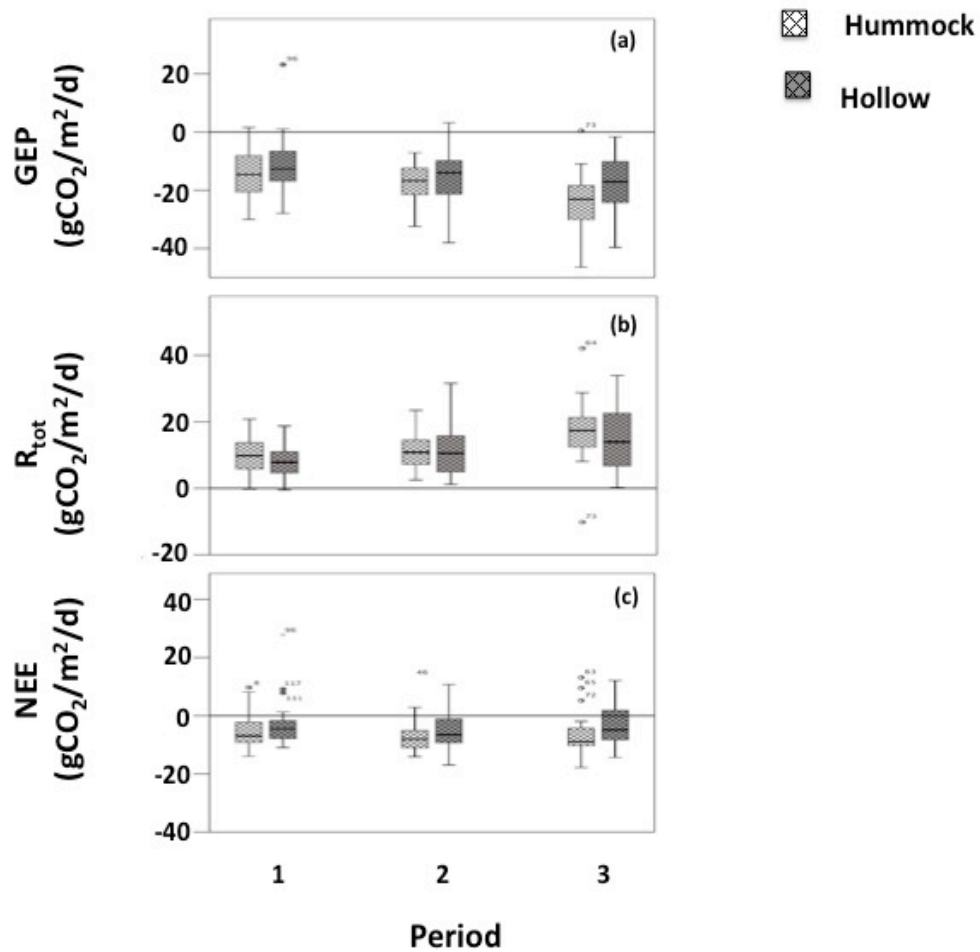
Figure 3.6: Box plots of temporal and spatial variations in GEP (a), R_{tot} (b) and NEE (c). Where temporal patterns are characterized by the three incubation periods (x-axis) and microforms are differentiated by the colour of each box, where white-hatched boxes represent hummocks and dark-hatched boxes are hollows. Carbon dioxide uptake is indicated when the flux value is negative and release of CO_2 is indicated by a positive flux value.
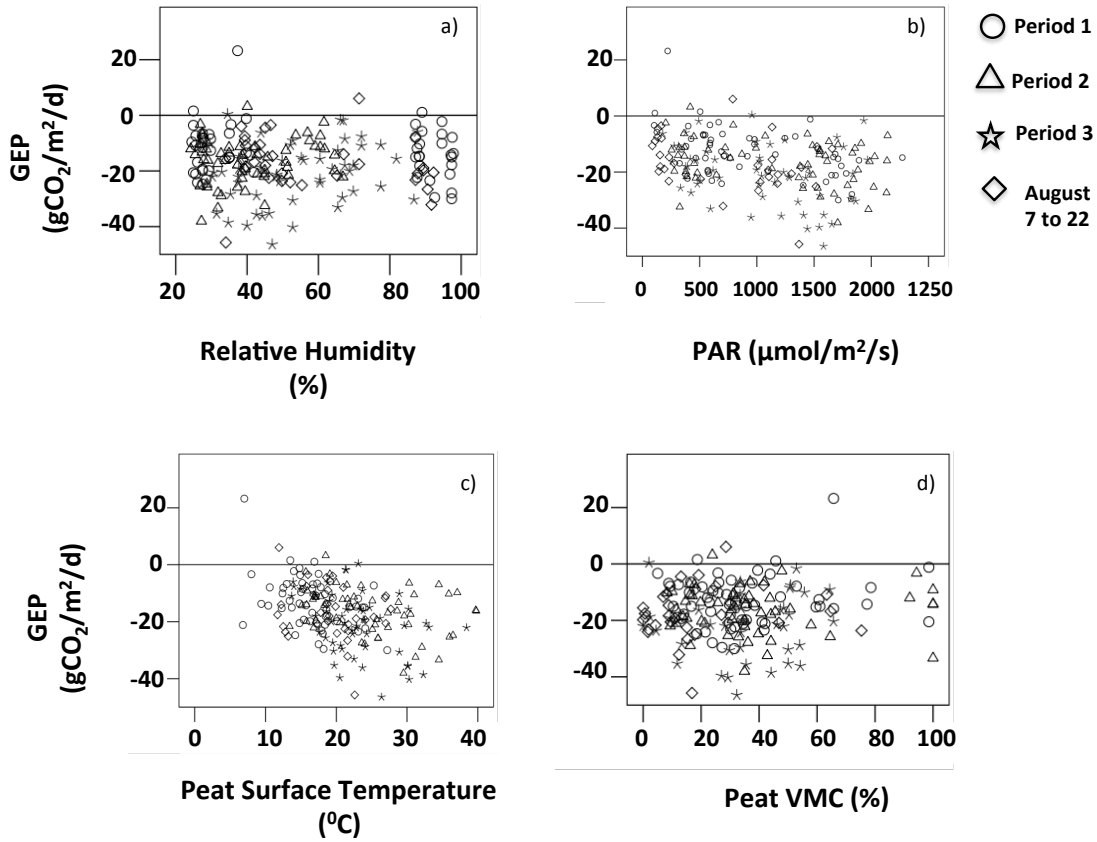
Figure 3.7: Relationship between GEP and relative humidity (a), PAR (b), peat surface temperature (c) and peat moisture (d) across three incubation periods. Relative humidity is ambient RH measured within 30min of GEP chamber measurements. An average PAR value was measured over 5 minute intervals with GEP chamber measurements and peat surface temperature and peat VWC were measured at the time of GEP chamber measurements. Carbon uptake is indicated by negative rates and carbon release is shown with positive values.
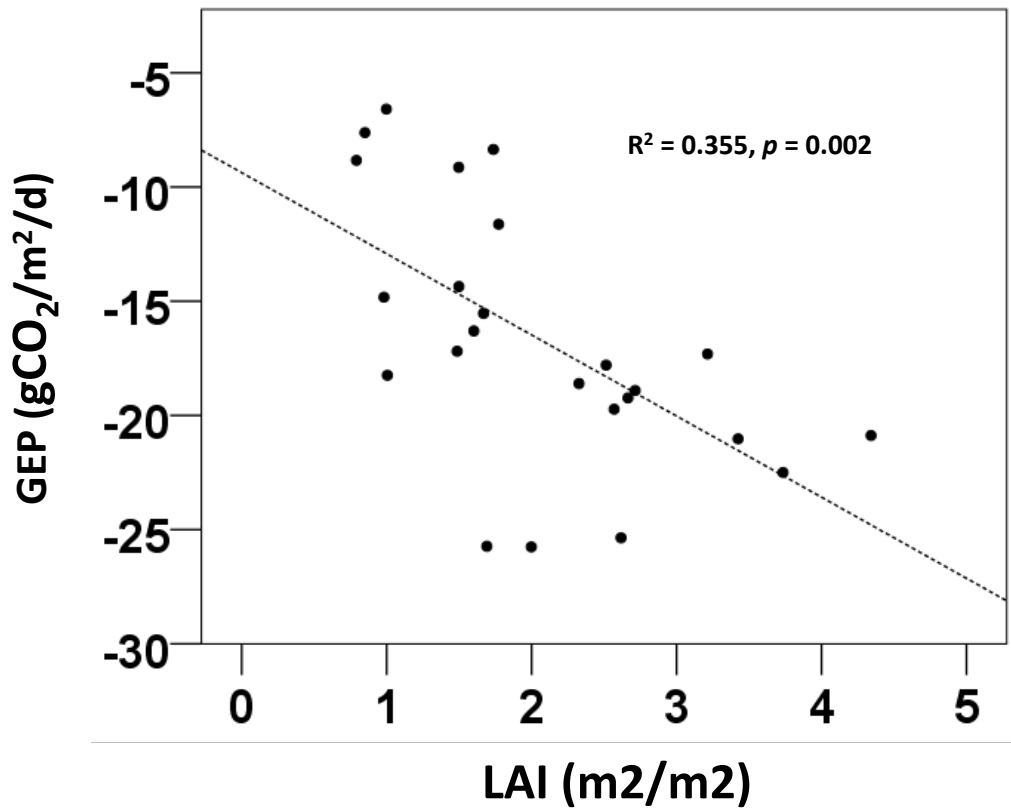
Figure 3.8: Relationship between median GEP (y-axis) and total leaf area index (LAI) of vascular species. Each point on the figure represents an individual chamber of the study site (N =24).
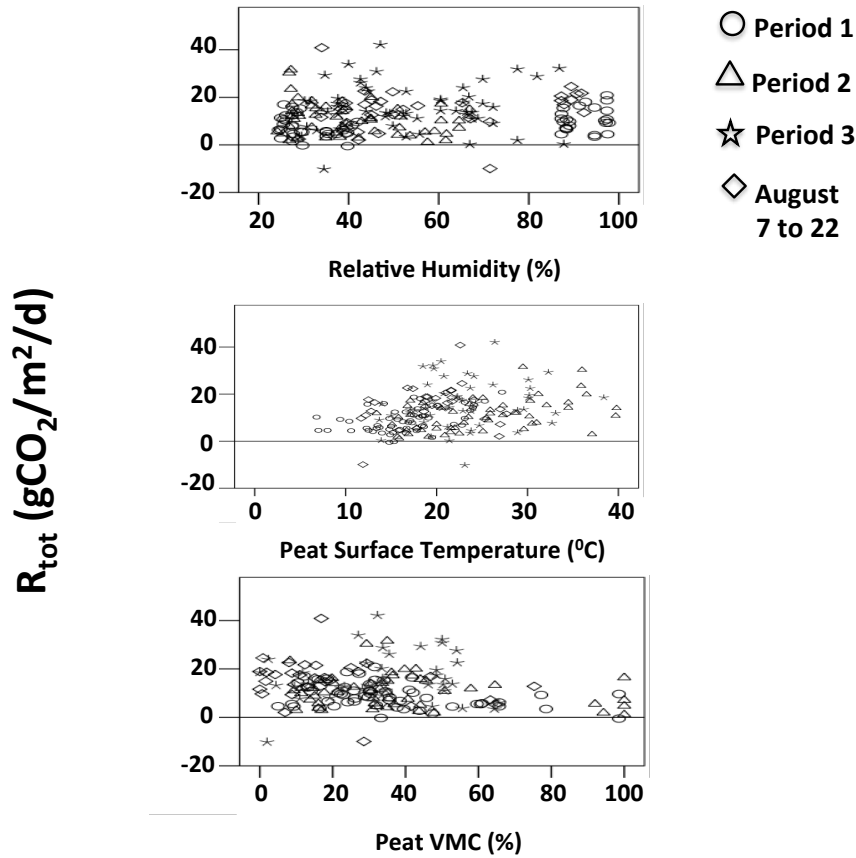
Figure 3.9: Relationship between respiration and relative humidity (a), peat surface temperature (b) and peat moisture (c) across the three incubation periods. The relative humidity used in figure (a) is ambient RH, measured within 30min of GEP chamber measurements. An average PAR value was measured over 5 minute intervals with GEP chamber measurements Peat surface temperature and peat VWC were measured manually with respiration chamber measurements. Positive respiration values represent CO_2 release and negative values indicate an uptake of CO_2.

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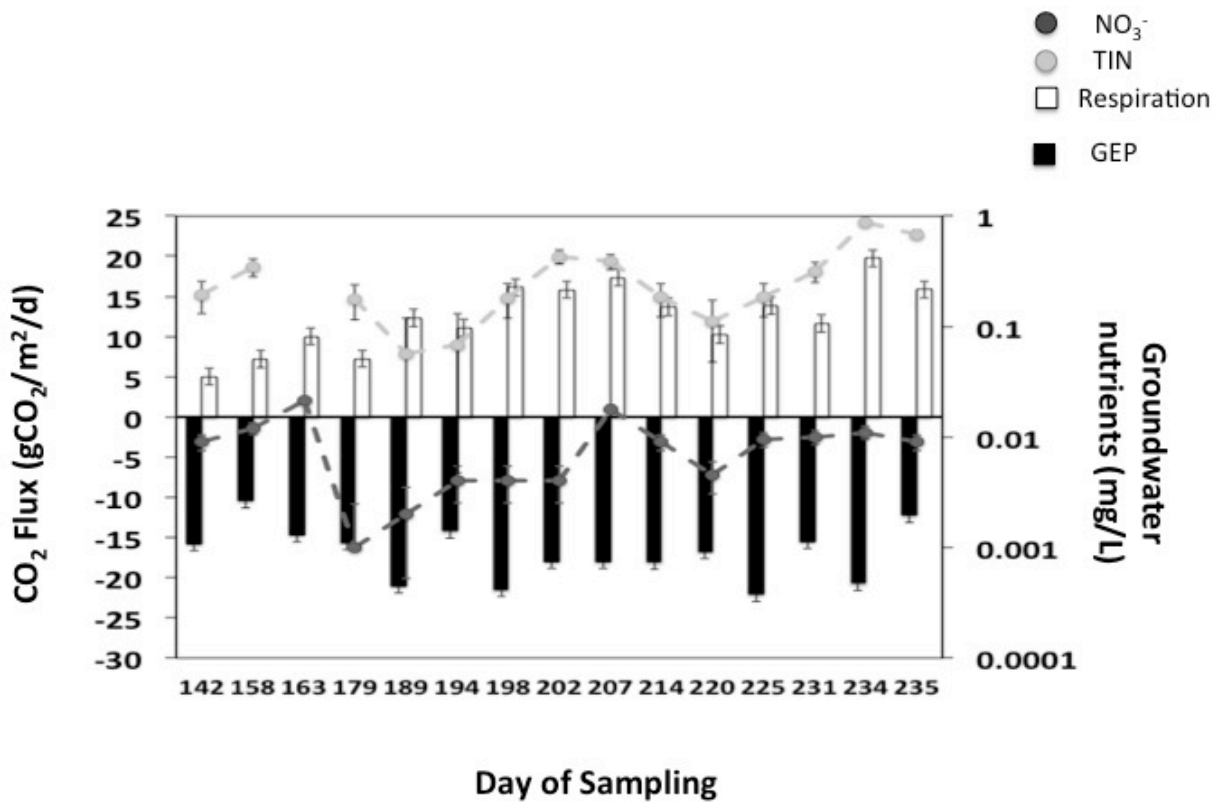
Figure 3.10: Comparison of seasonal variation in groundwater N (second y-axis) and CO_2 flux rates (first y-axis). Dissolved groundwater nutrients are shown on a logarithmic scale and include median daily concentrations of NO_3^- (mg/L) the dark markers and TIN (mg/L), the light markers. CO_2 flux rates (gCO_2/m^2/d) include GEP (dark bars) and respiration (light bars) and are shown in median daily values. Sampling days of groundwater nutrients and CO_2 flux measurements are shown on the x-axis.

Impacts of a semi-permanent road on N and CO2 dynamics

The reclamation area had no significant impact on N or CO_2 dynamics thus data were grouped by north (dry) and south (wet) of the road to determine the effects of disturbance on nutrient and CO_2 cycling.

The semi-permanent road impeded shallow groundwater movement from the south to north of the study site. The south side of the road was consistently wetter than the north side throughout the season, as seen in elevated water levels ($F(1,138) = 128.478$, $p < 0.001$, Figure 3.11a), and peat moisture ($U = 5778.000$, $p = 0.010$) (Figure 3.11b). An increase in both water table depth and peat moisture on both sides throughout the season, but VWC differed slightly between the two sides of the road in Period 3 (Figure 3.11). Differences in peat VWC between the two sides were observed among microforms, where peat VWC in hummocks on the south ranged from *Mdn* 32 to 37% compared to a *Mdn* range of 17 to 33% in hummocks located on the north side, greater moisture differences between the two sides were observed among hollows, where moisture content in hollows located to the south of the road fell between *Mdn* 45 to 73% and hollows on the north side had a range of *Mdn* 41 to 51%.

Differences in water levels and moisture had effects on redox potentials (determined by PRS probes). The south side (wet side) hollows had lower redox and were characterized as anoxic having seasonal Fe and Mn concentrations of *Mdn* 29.4 and 28.8 mg/m^2/3 weeks, respectively. The anaerobic conditions and low redox potential was unique to south side hollows and differed significantly from the redox potential of hollows located to the north of the road ($H(1) = 5.702$, $p = 0.017$ & $H(1) = 11.877$, $p = 0.001$, for differences in Fe and Mn concentrations, respectively). North side hollows were aerobic

(*Mdn* 3.6 and 8.5 mg/m^2/3 weeks in Fe and Mn, respectively). The higher redox in hollows on the north (dry) side were comparable to those found in hummocks on both sides of the road.

Groundwater N (NO_3^- and TIN) concentrations were consistently greater on the drier side (north) throughout the season ($U = 1840.000$, $p < 0.010$, NO_3^- & $U = 1648.500$, $p < 0.001$, TIN, Figure 3.11c,d). In contrast, ext-NO_3^- and TIN pools were greater on the wet side (south) in Period 2 ($U = 5.000$, $p < 0.001$ & $U = 13.000$, $p = 0.001$) but marginally lower on the wet side when ext-N pools were at a seasonal high during Period 3 (Figure 3.11). The road did not affect net N mineralization rates ($H(1) = 2.609$, $p = 0.106$, Figure 3.12), TIN supply rates ($F(1,72) = 0.279$, $p = 0.599$, Figure 3.12) or net nitrification rates ($U = 545.000$, $p = 0.328$) (Figure 3.13), but appeared to have a significant effect on NO_3^- supply rates (Figure 3.13). NO_3^- supply rates were greater on the dry (north) side during Period 3 ($F(1,72) = 8.082$, $p = 0.010$, Figure 3.13), which corresponds with greater N concentrations observed in the groundwater system during the same period (Figure 3.11). The greatest N concentrations in groundwater and NO_3^- supply rates were located adjacent to well pads and did not vary with proximity to the road.

CO_2 exchange rates did not vary between the two sides of the road and no interaction effects were found among incubation periods, microform or side of road (Figure 3.14).
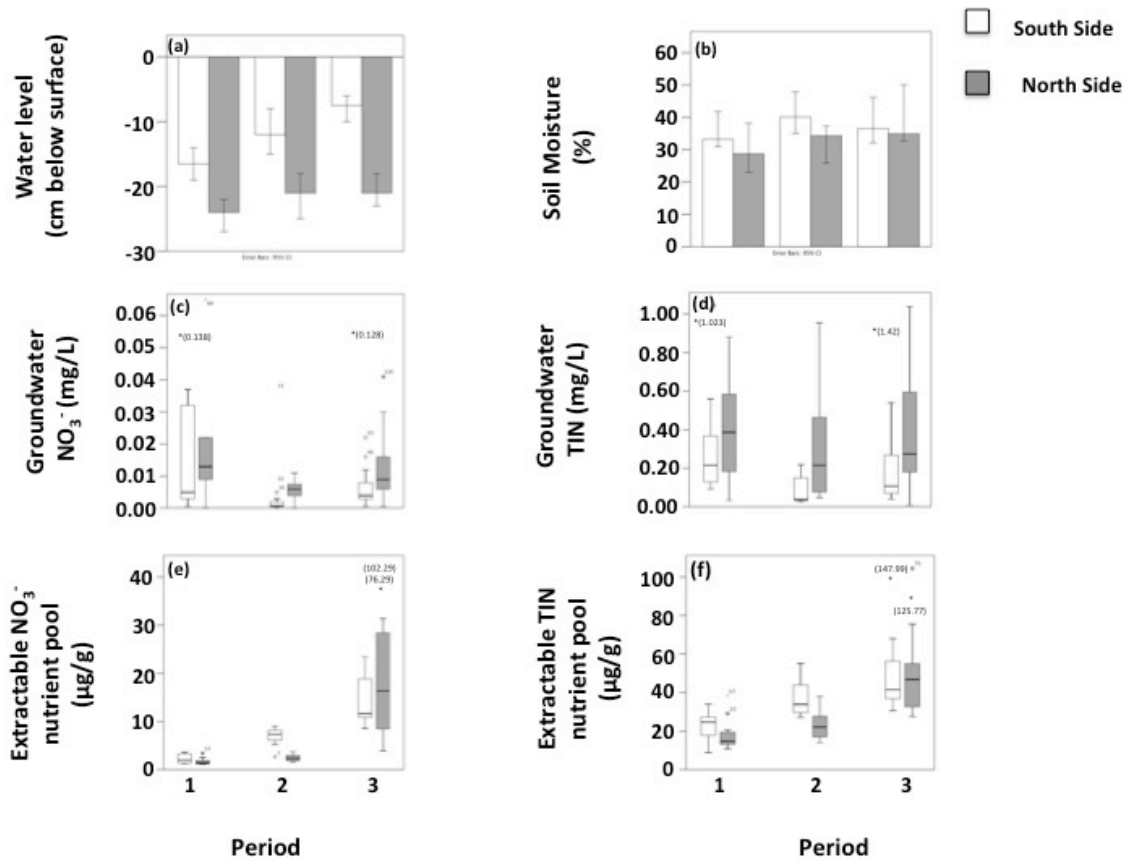
Figure 3.11: Comparison of moisture conditions, groundwater N and ext-N between the two sides of the site. Where variables are water level position (a), peat volumetric moisture content (b), nitrate concentration in groundwater (c), total inorganic concentration in groundwater (d), peat ext-NO_3^- pools (e), and peat ext- TIN pools (f). Water table depth and volumetric moisture content show median values with 95% confidence intervals. Measurements were collected throughout three incubation periods (x-axis). White boxes symbolize the south side of the road and dark boxes represent the north side.
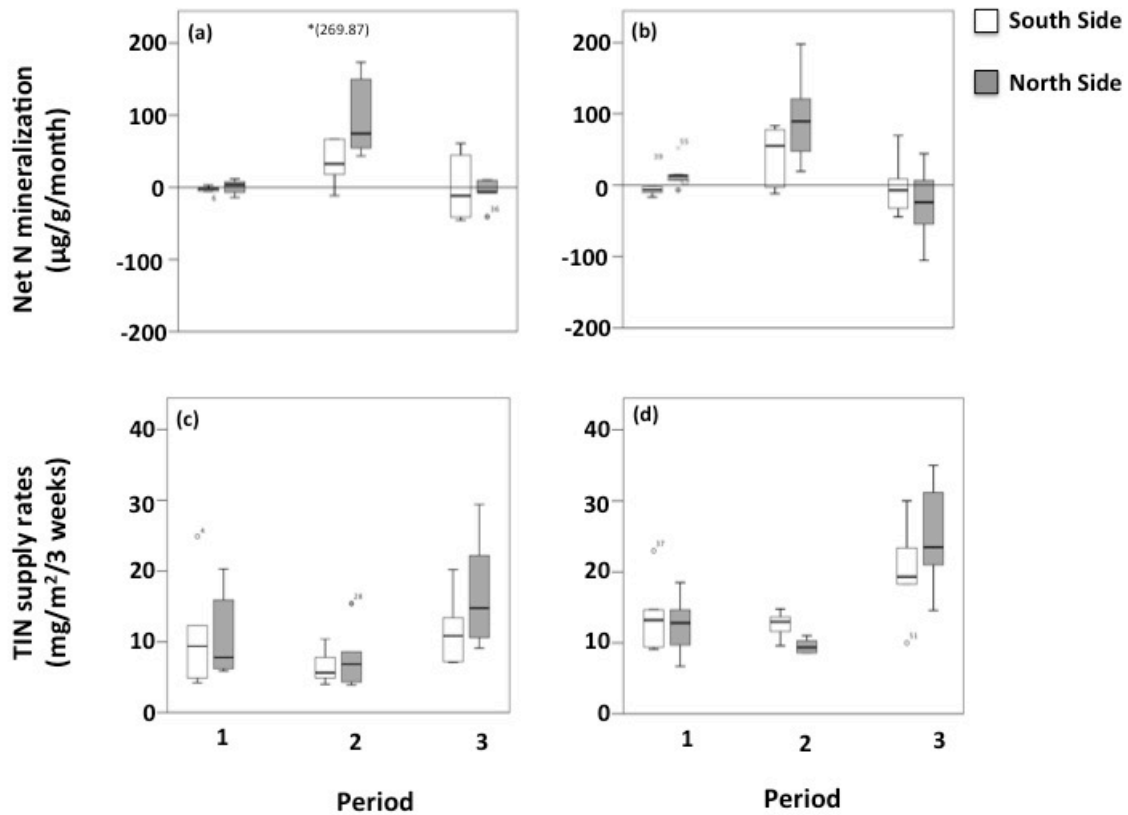
Figure 3.12: Comparison of TIN dynamics between microforms located on a north and south sides of the semi-permanent road. Net N mineralization rates (a) and (b) and available TIN after plant and microbial uptake (c) and (d) are studied to determine differences in N cycling between plots located to the south (white boxes) and north (dark boxes) of the road. The two processes are observed over three incubation periods (x-axis) and are separated by two microforms. N dynamics in hummocks are shown in figures (a) and (c) and figures (b) and (d) represent hollows.
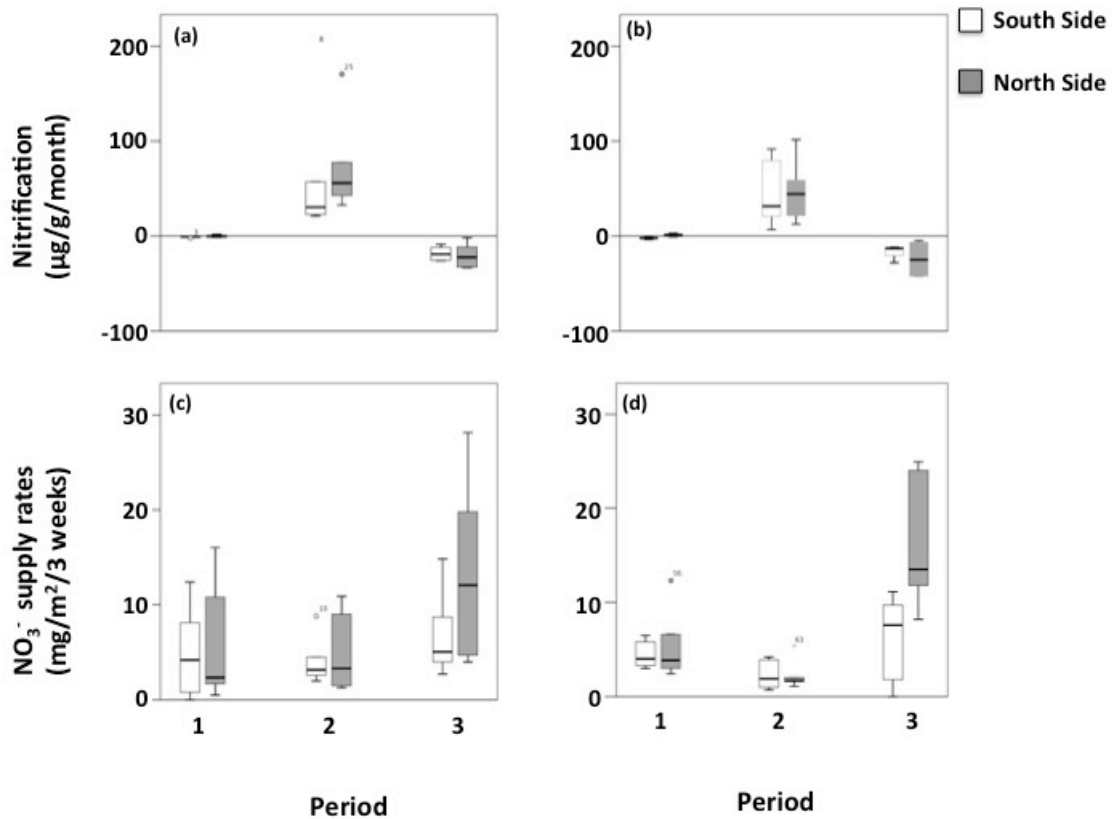
Figure 3.13: Comparison of NO$_3^-$ dynamics between microforms located on the north and south sides of a semi-permanent road. Two processes are looked at in the cycling of NO$_3^-$ over three incubation periods (x-axis), nitrification (figures a and b) and NO$_3^-$ availability after plant and microbial uptake (figures c and d). Processes are separated by microforms, where hummocks are on the left side of the figure (a and c) and hollows are shown on the right (b and d). Figures are further divided by plots located on the south (light boxes) and north (dark boxes) side of the semi-permanent road.
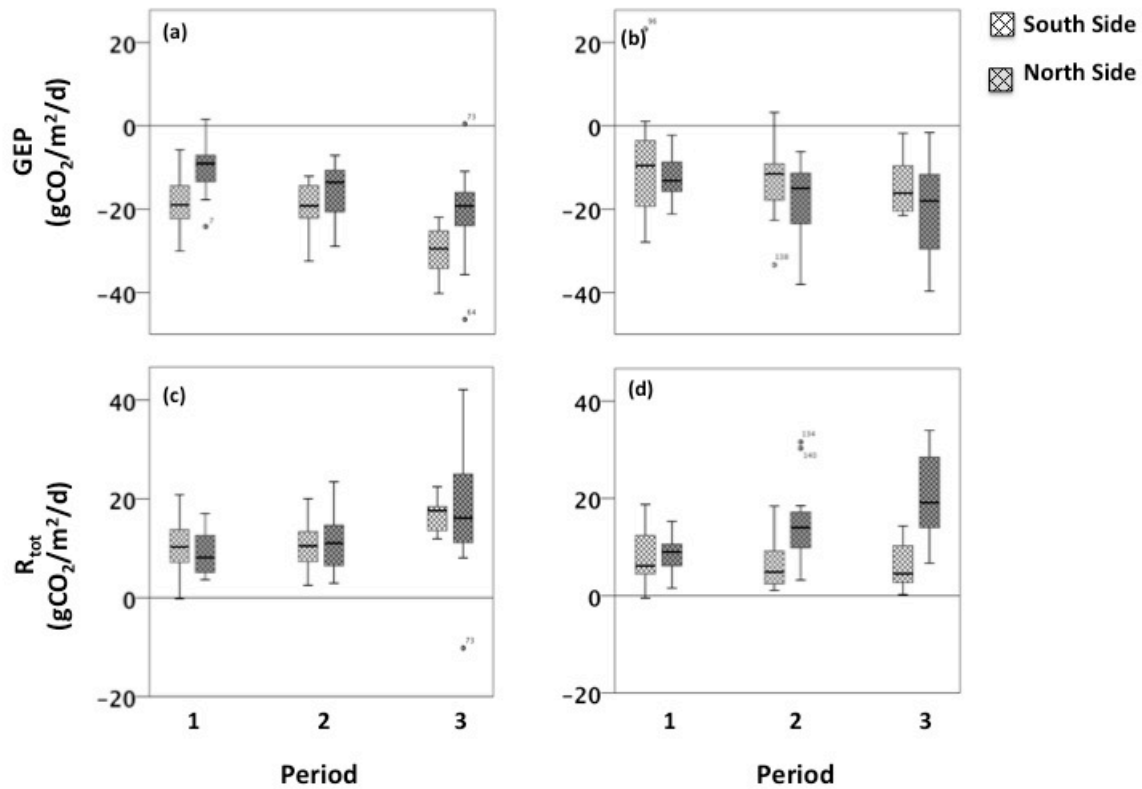
Figure 3.14: Comparison of CO_2 flux rates between microforms located on the north and south side of a semi-permanent road. Gross ecosystem production (a) and (b) was measured to determine differences in productivity between the site located to the south (white hatched boxes) and north (dark hatched boxes) of the winterized road. Respiration rates (c) and (d) determines if the road impacts the release of CO_2. The carbon flux rates were measured using an enclosed chamber, over three seasonal periods (x-axis) and separated by hummocks (a) and (c) and hollows (b) and (d).

Discussion

Nutrient Content and Terrestrial CO$_2$ Exchange

Nutrient content (N and P) and terrestrial CO$_2$ exchange at the JACOS site were not always comparable to other peatland studies. Nitrate and TIN pools at JACOS throughout June and July were similar to ext-N pools found in other WBP wetlands, however, N pools in late July to August (Period 3) were slightly higher (Macrae *et al.*, 2006). Seasonal net nitrification rates were immobilized (-1 µg/g/month), which is common for this region, where net nitrification rates are commonly immobilized or close to 0 (e.g. Wray and Bayley, 2008). In contrast to this, net N mineralization rates were low at JACOS in comparison to studies conducted in temperate peatlands (Macrae *et al.,* 2013).

There is limited information on P cycling in Boreal peatlands; however, studies of P in temperate Canadian peatlands suggest that seasonal WEP at JACOS were relatively high (e.g. Macrae, 2013) and the sizeable nutrient content at JACOS could be a result of contamination from the mineral materials used to construct the semi-permanent road and the well pads located on the JACOS fen.

Additionally, seasonal CO$_2$ flux rates at JACOS were more productive throughout the season than rates of productivity (NEE and GEP) found in a previous study, where R$_{tot}$ and GEP were not as balanced as in the current study. Unlike our system, this system (peatland-pond complex) had greater rates of R$_{tot}$ (more terrestrial CO$_2$ released) than rates of photosynthesis (GEP) resulting in NEE to be most productive in the early green season (system was a carbon sink) but then the overall system released CO$_2$ throughout the rest of the growing season (e.g. Solondz, 2008).

Seasonal variations in N, P and CO$_2$ dynamics

Seasonal trends in N dynamics (NO$_3^-$ & TIN) were related to temperature as N mineralization, nitrification and N supply rates increased with higher temperatures, resulting in larger peat extractable N pools (Holden, 2004). Throughout the coolest incubation period (Period 1), N content (ext-N and N supply rates) was the lowest and NO$_3^-$ and TIN were immobilized and/or at or near 0 μg/g/month however, groundwater N was high. In between Periods 1 and 2, ext-N pools increased as an effect of an external supply; because each pool was determined at the beginning of each incubation period, the increase in ext-N from Period 1 to Period 2 was not an effect of nitrification and mineralization rates but was most likely a result of available N from groundwater. In contrast to ext-N, N supply rates and groundwater N decreased between Periods 1 and 2 suggesting that available N was lost supporting vegetation growth throughout Period 2. Temperatures (air and peat) became significantly higher in Period 2, resulting in peak mineralization and nitrification rates, which contributed to large N pools and N supply rates in Period 3. Groundwater N was also high throughout Period 3, and most likely contributed to the highest NO$_3^-$ and NH$_4^+$ content in peat extractable pools during the season (Period 3).

Seasonal variations in P dynamics were limited to P supply rates, where P supply decreased throughout the season and was most likely a result of plant uptake. Richardson and Marshall (1989) observed similar findings, as they determined that inorganic P removal from peat was highest over the growing season.

CO$_2$ (GEP & R$_{tot}$) had similar seasonal trends to ext-N, where both plant productivity and respiration were driven by temperature and gradually increased

throughout the season. This has been observed in other poor fens, where temperature was determined the main driver in CO_2 fluctuations (Webster *et al.*, 2013). In addition to peat temperature, our results suggest that there is a significant correlation with vascular LAI and productivity, similar to Bubier *et al.* (2003), who found a significant positive correlation between the difference in NEE rates (measured when PAR > 1000) and foliar biomass ($r^2 = 0.79$; $p < 0.05$). Leaf area index peaked in mid July to August (Period 3) and likely explains why Period 3 released and sequestered the most CO_2 within the season. A significant effect of water level on CO_2 exchange was also not found, which contradicts many other studies that have determined water table level as a significant control on CO_2 fluctuations (Silvola *et al.*, 1996; Suzumigalski and Bayley, 1997; Alm *et al.*, 1999; Lahio *et al.*, 2003; Lafleur *et al.*, 2005; Chivers *et al* 2009). However, our finding may not be uncommon in poor fens as water table depth was found to be less important in poor fens where internal factors, such as temperature are the dominant drivers of CO_2 (Webster *et al.*, 2013). Temperature was also the main driver of N, resulting in and increase in N availability (Bonan and Van Cleve, 1992; Updegraff *et al.*, 1995; Mack *et al.,* 2004) and CO_2 (Schlesinger, 1997; Blodau 2002; Chivers *et al.,* 2009) throughout the season, where they peaked at the same time. P dynamics, however, did not follow the same trends and responded to high moisture and low redox conditions (Aldous *et al.,* 2005; Reddy and Delaune, 2008).

Spatial variations in N, P and CO$_2$ within the peatland

No differences in ext-N, N mineralization (and nitrification) and NO_3^- supply rates between hummocks and hollows are observed throughout the season. These results

contradict other findings that suggest N availability is greater in hummocks than hollows in drier (drained) sites (Macrae *et al.*, 2013) and in regions where evapotranspiration controls the hydrology (Eppinga et al. 2008). This finding suggests that the moisture differences between microforms were not great enough to affect N dynamics.

Unlike N, spatial variation between microforms in P dynamics were observed, where hollows had greater inorganic P than hummocks, likely the effect of anoxic conditions in hollows weakening the sorption of P in peat thus releasing inorganic P to biota (Gillian and Skaggs, 1981; Nicols, 1983, as cited in Richardson and Marshall, 1986). Studies have shown that inorganic forms of P, such as PO_4^{3-} have been released in northern peatlands through seasonal fluctuations in water table (Moore *et al.*, 2005), when, periods having anoxic and low redox conditions cause the conversion of Fe^{3+} to ferrous iron (Fe^{2+}), which in turn results in a release of inorganic P from oxyhydroxide flocs (Aldous *et al.*, 2005 and Crowley and Bedford, 2011). This could explain why WEP were higher in hollows than hummocks, as approximately half of the site's hollows had low redox potentials as well as anaerobic conditions throughout June to August (Periods 2 and 3).

However, the mineralization of P does not explain the spatial patterns between hummocks and hollows, as immobilization was favoured in hollows (Figure 3.9b). Literature has suggested that using the buried bag method to determine net P mineralization rates do not account for the rapid complexation of P with mineral constituents of peat (Schlesinger, 1997), therefore our net mineralization rates could be underestimated. Furthermore, the relatively high groundwater and WEP suggest that there may have been a generous external mineral source supplying P to the system, a finding not

uncommon in fens and implies that the system is not P limited (Schlesinger, 1997). The source of P from groundwater could have been sufficient enough to compensate for the immobilization observed in hollows.

Although, productivity (GEP), NEE and respiration varied between microforms, where hummocks appeared to be more productive and appeared to respire more than hollows, the differences were not statistically significant. This finding suggests that moisture differences between microforms were not great enough to have a significant effect on CO_2 exchange (Solondz *et al.,* 2008).

Relationship between N and CO_2

While there is no statistical support to suggest that direct relationships existed between N and CO_2, some general relationships were observed, where N and CO_2 dynamics demonstrated parallel trends throughout the season. For example, peaks in GEP rates, ext-N pools and N supply rates were all observed across incubation Period 3 (Figures 3 and 7). Furthermore, the initial peak in GEP was observed in Period 2 (Figure 3.7a), overlapping with peaks in net N mineralization rates (Figure 3.3b) and a possible surge in plant uptake (Figure 3.3c). This could be a result of N and CO_2 having similar reactions to environmental controls, such as temperature, where a rise in peat temperatures between Periods 1 and 2, resulted in peak mineralization rates (Bonan and Van Cleve, 1992; Updegraff *et al*., 1995; Mack *et al.*, 2004) and an increase in productivity (Blodau, 2002; Chivers *et al.*, 2009) and respiration (Schlesinger, 1997). The visual trends could also be showing an important indirect biogeochemical relationship, where the increase in N supply and availability to plants, resulted in a surge in plant growth (increase in LAI) and

therefore an increase in productivity. This can be seen with both, internal and external N supplies, where plants could have been receiving an internal supply of N, in Period 2 (peak mineralization) and then used N supplied via groundwater in Period 3, when N was immobilized but ext-N pools and groundwater N remained high.   The ability for *Sphagnum* spp. to acquire N from internal and external sources when necessary has been observed by Bridgham *et al.* (1999), as cited in Limpens *et al.,* (2006), where the uptake of nutrients from pore water in peatlands having high evapotranspiration rates can contain the sufficient amount of N necessary for growth.

Ultimately, our results suggest that N and CO_2 did not have direct relationships. However, determining relationships between variables within the field has been found to be challenging as the response of CO_2 to specific variables, such as N supply is difficult to separate from the response of CO_2 to other daily variables (Aerts and Ludwig, 1997; Blodau, 2002 and Knorr *et al.*, 2009). For example, we found that not all environmental drivers were the same in N and CO_2 dynamics, where GEP and respiration rates in hollows were sensitive to moisture conditions, which had no effect on N dynamics. This difference could have caused difficulties in finding direct relationships between N and CO_2, for the moisture threshold affecting these two dynamics were different. Consequently N could not be considered a control of productivity, but rather other environmental variables, such as PAR, peat temperature and LAI were the dominant factors in determining the productivity of this system.

Effects of a semi-permanent road on N dynamics

The unpredictable effects of the road on N dynamics could be explained by direct and indirect impacts of the road. The possible restriction of groundwater flow from the south to the north side had an impact on groundwater N concentrations, leading to greater N concentrations in groundwater on the drier side (north) of the road. The greater groundwater N content on the north side could be related to nutrient hotspots at plots located close to decommissioned well pads that were once used in the oil extraction process. The mineral caps of well pads have the potential to leach into peat and change the chemistry of a peatland (Graf, 2009). The effects of the road on groundwater nutrients, water level, moisture and redox could have indirectly caused the moderate impacts on ext-N. In Periods 1 and 2 (late May to July), the south side of the road had greater ext-N pools than the north. However, there was a lower external supply of groundwater N on the south side of the road and comparable internal N supply via net mineralization rates to the north of the road. This suggests several things including 1) an unknown source was supplying the south side of the road; or 2) N was lost on the north side by possible plant uptake. In the following incubation period (Period 3, mid July to early August), ext-N pools were higher on the north side, which could have been a result of the larger external influx of N in groundwater in conjunction with internal N supply such as mineralization and/or greater N uptake by plants. Even though no significant differences in N transformation rates were determined between the sides of the road, peak mineralization rates throughout June to July (Period 2) are higher on the north side, which appear to be a result of lower water level and drier moisture conditions. The south (wet side) had greater *Sphagnum* biomass (Table 3.2), which could have lead to lower ext-N and N supply rates on the south side

because *Sphagnum* spp. are known to outcompete nearby plants and microbes for N (Zoltai and Vitt, 1995; Jonasson and Shaver, 1999 and Turetsky, 2003). Moreover, the higher external N supply on the north via groundwater in Period 3 and greater internal supply on the south (mineralization rates) in Period 2 along with greater plant uptake on the south side, can also account for the slightly higher NO_3^- supply rates found on the north side.

Although the south side had higher water levels, wetter moisture content and anaerobic conditions (observed in hollows) there appeared to be limited impact on N transformation rates. Thus, threshold conditions in water level, peat moisture and redox were not reached. Additionally, bulk density in the upper 20 cm of the peat layer were similar between the north and south side of the road (Table 3.1) and could have been a strong factor in why N transformation rates remained relatively low and constant between the two sides.

Effects of a semi-permanent road on CO_2 dynamics

The low impact of the road on CO_2 dynamics was most probable because the environmental factors controlling CO_2 flux rates were uniform across the road including PAR, peat temperature, air temperature, vascular biomass and LAI. As a result, no statistical differences were found in CO_2 exchange rates between the north and south side. However, the south side (wet) hummocks were the most productive, and hollows on the northern side (dry) were more productive than the least productive south hollows (wet). Although these differences were insignificant, the observations do suggest that the road did have a slight impact on GEP. For example, the greater productivity in hummocks on

the south side is most likely related to differences in vegetation biomass and species composition between the south and north side of the road, as south side hummocks are covered with more *Sphagnum* moss (Table 3.2) (Bubier *et al.*, 2003).

There were apparent differences in R_{tot} between the wet (south) and dry (north) side of the road, where hollows respired less than hummocks. This could be a result of a moisture threshold between the two microforms when south side hollows were flooded throughout several days (Alm *et al.*, 1999). However, these differences were not significant.

Conclusions

Seasonal and spatial patterns were not comparable between nutrients. N dynamics varied seasonally, peaking with temperature, plant growth and uptake but did not vary spatially between microforms and the response to the road was inconsistent among N forms. Differences between the two sides of the fen were found in groundwater N (NO_3^- & NH_4^+), NO_3^- supply rates and in ext-N. However, no effects of the road were found on net N mineralization or net nitrification rates suggesting that lower peat moisture and water table position on the north side did not reach the thresholds needed to increase microbial activity and N mineralization.

Unlike N dynamics, P dynamics were inconsistent throughout the season and differed between microforms. WEP and P supply rates were affected by differences in redox potential between microforms, where hollows had low redox potential, anoxic conditions and greater P concentrations. Seasonal variation in available P (as determined by PRS probes) suggests inorganic P made available to plants and microbes is not only driven by redox but also by plant growth. In contrast to this, net P mineralization rates

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remained consistently low throughout the season and between microforms, however, our mineralization values maybe underestimated and dampened actual seasonal and spatial effects.

Carbon exchange was found to vary seasonally, but differences in microtopography had no effect on productivity, NEE or respiration. Moreover, the road had no statistical effect on GEP rates or on R_{tot} however, the variations observed between the wet and dry side of the fen suggest that the effects of the road on peat moisture and water level lead to slight differences in plant communities and complicated CO_2 fluctuations.

Correlations having CO_2 fluctuations with environmental variables confirm the importance of PAR, temperature, peat moisture, and LAI (species composition) on CO_2 dynamics. The inter-couplings and interrelationships among these factors show how complex peatland systems are and suggest that direct relationships between two factors such as N and CO_2 are difficult to determine in the field.

Future studies should continue to examine extractable nutrients, net nutrient transformation rates and nutrient availability in peat yet include gross mineralization, direct microbial and plant uptake, leaching in runoff as well as more appropriate methods for determining ext-P and P mineralization rates in order to fully understand the specific pathways nutrients take within a poor fen. A complete CO_2 study with direct measurements of plant growth would provide a better indication of the fen's productivity and a better understanding of how microtopography and disturbance by infrastructure affect CO_2 dynamics. Additionally, future studies should examine nutrient and CO_2 cycling over multiple years to determine the interannual variability and to assess the long-

term effects a road may have on peat moisture, water table position and vegetation communities. Future studies should compare the effects of multiple semi-permanent roads that vary in size and location across different peatland types to better understand and predict how roads developed by the oil industry will affect the function of peatlands within the WBP.

Nonetheless, the current study suggests that seasonal trends in N, P and CO_2 are driven by different environmental variables. Additionally, the study confirms the influence that seasonal variation in temperature and plant composition has on N and CO_2 dynamics and that the effects of microtopography are less significant in nutrient cycling than CO_2 dynamics. Infrastructure development such as a semi-permanent road and its effect on a system's hydrology had low to moderate impacts on N supply and CO_2 flux rates in our study; however, effects are difficult to predict due to complex interrelationships among N, CO_2 and dominant biotic and abiotic drivers. Furthermore, it should be noted that available nutrient content within JACOS was high in comparison to other studies and albeit low net mineralization rates. This suggests there is unique external source of available nutrients supplying the system, which could be groundwater nutrients and/or contamination from the mineral sediments of the road and nearby well pads. This is speculation, and future research should focus on comparing nutrient content of disturbed and pristine WBP peatlands to determine contamination of linear disturbances.

Chapter 4

Spatial Variation in Nutrient Dynamics Across Five Different Peatland Types in the AOS, Following a Moisture Threshold

Introduction

The Western Boreal Plain (WBP) of Canada covers 7 % of Canada (737, 800 km^2; Wiken, 2010) including the Athabasca Oil Sands region (AOS), varying in land cover and hydrology. 30 to 50 % of the WBP is covered with peatlands (Vitt *et al.*, 1995; Wray and Bayley, 2007) making this region important to the global carbon (Gorham, 1991) and nitrogen cycles (Wray and Bayley, 2007). The WBP encompasses the Athabasca oil sands region (AOS) in Northern Alberta, where oil and energy related industries are affecting these important ecosystems on a large scale.

To offset the disturbances on wetland systems within the oil sands region, the government requires that decommissioned oil wells, surface mines and linear disturbances be restored. However, a strict set of guidelines for reclamation practices have yet to be encouraged (ASRD 2007; Reclamation Criteria Advisory Group 2008, as cited in Graf, 2009) and the current criteria do not provide standards that can be used to evaluate the success of reclamation practices (Foote, 2012). Furthermore, companies are not enforced to restore post-mined areas back to their natural (pre-mined) ecosystems and the loss of these systems could lead to the release of stored C and reduce the amount of C that is currently being sequestered (Rooney *et al.*, 2012). The need to restore peatland systems is even more imperative with the effects of climate change (Graf, 2009). However, peatland

restoration has been found to be difficult and faces a number of limitations in predicting nutrient dynamics, drainage and survival of peatland vegetation, which is uncertain where post-mined environments could have high concentrations of salts, metals and naphthenic acids (Rooney *et al.*, 2012).

Baseline data on pre-mined surface cover is limited in this area making reclamation development even more difficult. Therefore studies and extended knowledge on how natural peatlands within this region function are necessary to determine the appropriate vegetation and critical processes that are needed to successfully reclaim an area. Fortunately, many natural sites having similar land cover to the pre-mined areas are still intact within the Athabasca area (Foote, 2012) and can be used as reference sites to study the critical ecohydrological processes involved in peatland function, such as nutrient dynamics.

Nutrient dynamics within northern peatlands are complex. It is commonly suggested that nutrient availability follows a hydrogeochemical gradient, where rich fens, which have lower pH and greater influx of mineral sourced water, are believed to have greater nutrient availability than ombrotrophic bogs (Bridgham *et al.*, 1996) believed o have lower nutrient inputs (Bridgham *et al.*, 1998). Although there are many studies that support this theory (e.g. Moore and Betlamy, 1974, Damman, 1986, as cited in Bridgham *et al.*, 1996) there are also many studies that contradict these findings, where bogs have been found to have higher nutrient availability than fens (Verhoevan *et al.*, 1990; Bridgham *et al.*, 1998; Kellogg and Bridgham, 2003; Mettrop *et al.*, 2014) and some findings have found that nutrient cycling does not differ across peatland types (Vitt, 1990). Other studies have suggested that nutrient dynamics such as N and P mineralization are

not driven by a minerotrophic-ombrotrophic gradient but instead by natural variations in site hydrology, redox potential (Bridgham *et al.*, 1998, Mettrop *et al.*, 2014), bulk density, microbial demand (Mettrop *et al.,* 2014) and vegetation (Kellogg and Bridgham, 2003). Moreover, N and P have been found to respond differently to similar environmental controls across different peatland types (Bridgham *et al.*, 1998; Mettrop *et al.*, 2014). These inconsistent findings suggest that the characterization of nutrient dynamics across a range of peatland types in the AOS is imperative to understand the processes involved in nutrient cycling within this region to determine if peatland type has an effect on nutrient dynamics and infer how hydrologic disturbance may affect nutrient dynamics and supply in the region. This knowledge can then be applied to the development and management stages of fen reclamation projects.

The goal of this study is to characterize spatial differences in nutrient (nitrogen (N) and phosphorus (P) transformations and supply rates within 5 different peatlands within the AOS in Northern Alberta. In this study, N and P availability and net mineralization rates throughout the period when vegetation growth is expected to be at its highest (July) are quantified within and across different peatland types along a hydrological and vegetative gradient in the WBP. It is hypothesized that variation within sites will be found between microforms, where hummocks will have greater nutrient availability relative to hollows (Eppinga *et al.*, 2008). It is expected that the effects of a minerotrophic gradient on the spatial variability in nutrient dynamics among sites will be small (Bridgham *et al.*, 1998; Kellogg and Bridgham 2003) and environmental variables, such as water table position and peat moisture will be the key drivers in nutrient cycling.

Materials and Methods

Study Sites

Research for this study was conducted in five different peatlands that ranged in vegetation biodiversity and disturbance (Figure 4.1). The peatlands were located in the AOS region of northern Alberta and included two bogs (one natural and one drained), a rich fen and two poor fens. The two bogs were located in Wandering River, approximately 200 km South of Fort McMurray, Alberta. One bog here was untouched and natural, hereafter referred to as WR N (55^0 21' N, 112^0, 31' W) and another a drained bog (WR D; 55^0 17' N, 112^0 28' W), where the water level had been lowered ten years prior to the study resulting in a 70 cm lower water position than WR N. Dominant vegetation cover of WR N included *Sphagnum* spp., *Rhododendron groenlandicum* (labrador tea), *Vaccinium vitis-idaea* (large bog cranberry), *Rubus chamaemorus* (cloudberry) and *Picea mariana* (black spruce). WR D had very little moss cover and comprised of *Cladonia spp.* (lichen) such as *Cladonia stellaris* (reindeer lichen) and *Clandonia spp.* (cup lichen), *Rhododendron groenlandicum*, *Vaccinium vitis-idaea* and *Picea mariana*. Poplar Creek Fen, hereafter referred to as POP, was a rich fen located 20 km north of Fort McMurray, AB (56^0 22' N, 111^0 14' W) and had vegetation cover dominated by *Larix laricina* (larch), *Betula glandulosa* (dwarf birch), *Equisetum fluviatile* (swamp horsetail), *Smilacena trifolia* (three-leaved Soloman's-seal), *Carex* spp. and moss including *Polytrichum* spp.*, Tomenthypnum* spp. and *Sphagnum* spp. (Borkenhagen, unpublished). One of the two poor fens was located on the Japan Canada Oil Sands (JACOS) Hangingstone In-situ Extraction site, 50 km south of Fort McMurray (56^0 19' N, 111^0 39' W). The fen was bisected by 450 m semi-permanent road constructed in 2001, which possibly restricted the

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flow of ground and surface water from the south to north sections of the fen. The fen was covered with *Sphagnum* spp. and had few other non-vascular species such as *Polytrichum* spp., *Cladonia Stellaris* and *Clandonia* spp. Vascular species that were common included *Rhododendron groenlandicum* and *Vaccinium vitis-idaea*. Pauciflora fen was the second poor fen studied and was situated 40 km south of Fort McMurray (56^0 56' N, 111^0 33' W). This fen comprised of *Carex limosa* (mud sedge), *Carex aquatalis* (water sedge), *Sphagnum* spp., *Betula glandulosa* (dwarf birch), *Oxycoccus microcarpus* (small bog cranberry), *Chamaedaphne calyculata* (leatherleaf) and *Andromeda polifolia* (bog rosemary) (Borkenhagen, unpublished).

Methods

Sampling Design

Each site contained two microform types: hummocks (microtopographic highs) and hollows, which are lower depressions in the terrain. Six replicate cores were extracted from hummocks and hollows within each of the sites, with the exception of the JACOS and Wandering River sites. The Wandering River site has been split by the drained and control sections for this study, and consequently the WR D and WR N sites have 3 replicates each. Ten replicates were extracted at the JACOS site in conjunction with a separate study. Cores were used to determine nutrient supply (extractable N and P) and transformations (net mineralization) over a three-week incubation period in July 2012. This time period was selected because it was considered to be the peak of the growing season and therefore representative of maximum transformation rates as has been reported in other studies (e.g. Macrae et al., 2013). The three-week incubation periods were staggered over several days across the peatlands, as it was not logistically possible to

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collect and process samples across the sites within a single day. The 3-week periods for each peatland were as follows: July 6 to July 27 (JD 188 to 209) at PAC, July 8 to July 29 (JD 190 to 211) at POP, July 9 to July 30 (JD 191 to 212) at WR N and WR D and July 16 to August 7 (JD 198 to 220) at JACOS.

Nutrient Supply and Cycling

Extractable pools and net mineralization rates of N and P (and net nitrification) were determined by collecting a set of peat cores (paired) from the upper 10 cm peat layer (live vegetation was removed from core) using a galvanized pipe (10 x 10 x 10 cm) and serrated knife to minimize compression of the peat. Of each pair of cores taken, one core was used to determine extractable nutrient pools, and the second "paired" core was placed in a polyethylene bag to exclude plant roots and lateral seepage/leaching, and incubated in the hole from which it was removed (after Eno, 1960 and Macrae et al., 2013). After the three-week incubation period, incubated cores were retrieved from the field and brought to the laboratory for the determination of extractable nutrient concentrations in the forms of nitrate (NO_3^-), ammonium (NH_4^+) and total inorganic nitrogen (TIN = NO_3^- + NH_4^+). Net nitrification, and net N and P mineralization rates were determined by subtracting the respective extractable nutrient concentrations from samples collected at the beginning of the incubation period from extractable nutrient concentrations in the paired cores at the end of the three-week period.
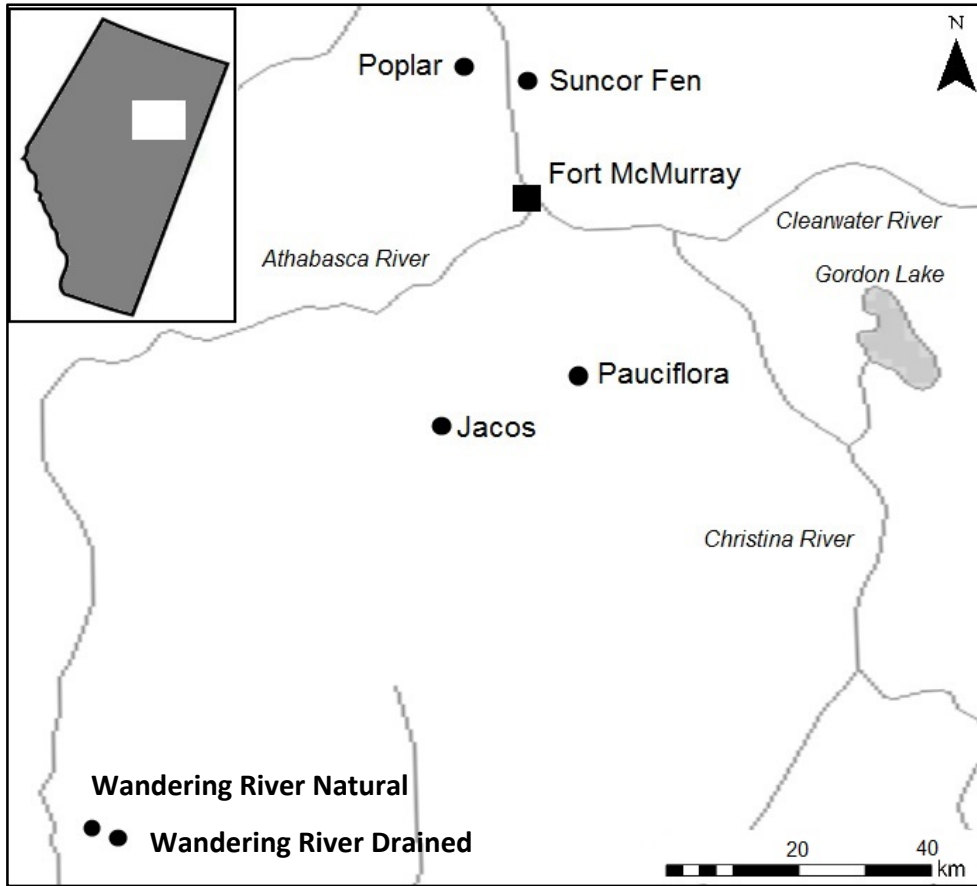
Figure 4.1: The five different peatland types studied for nutrient content throughout July 2012, where Poplar Creek fen is a rich fen, Pauciflora and JACOS are two poor fens, Wandering River N is a natural (undisturbed) bog and Wandering River D is a drained bog. Each site is in the Athabasca Oil Sands region of AB, Canada (the inset) and Fort McMurray is north of the study sites.

In cases where samples were collected from anoxic conditions, effort was made to remove oxygen from polyethylene sampling bags to prevent the introduction of oxygen to samples prior to extractions taking place. Samples removed from the field were stored in a cooler on ice until extractions were conducted within 12 to 24 hours of removal. In the laboratory, samples were hand mixed until homogenized. Two sub-samples of ~ 10 g (wet weight) were removed from each sample (from four corners of the sample bag). KCL and DI water extractions were then carried out following methods adapted from Brinkley and Hart (1989) for determination of N species and determination of water-extractable P (WEP). Extractions were conducted on field moist samples as drying samples can enhance extractable nutrient levels (Pote et al., 1996). To express extractable nutrients in per unit dry weight of peat sample, peat moisture contents were determined in the field at the time of sampling using calibrated (gravimetrically) Hydro-sense (Campbell Scientific, Canada) and theta moisture (Delta T Devices, England) probes. Colorimetry was used to determine the N and P content of each extractable sample at the University of Waterloo (Bran Luebbe AA3, Seal Analytical, Seattle, U.S.A., Methods G-102-93 (NH_4^-), G-109-94 (NO_3^- +NO_2^-), G-103-93 (SRP))

N and P supply rates were estimated in the field using plant root simulator probes (PRS probes; Western Ag. Innovations, Canada) at the same time as the buried bag incubations. PRS probes remain in cation and anion pairs that are incubated in the soil to determine the remaining nutrients available in soil after plant and microbial uptake. Each study plot contained 4 PRS probe pairs, which were incubated at 10 cm depths for 3 weeks in adjacent microforms, following methods provided by Western Ag. Innovations (2010).

Following the 3-week incubation, the probes were removed from the field and the four pairs corresponding to the same microform and study plot were placed in polyethylene bags. Within 24 to 72 hours of removal, probes were rinsed free of peat or vegetation, placed in new polyethylene bags and stored in a cool dry location until shipped to Western Ag Innovations for analyses of major cations (NH_4^+ Ca^{2+}, Mg^{2+} and K^+), anions, micronutrients and metals (NO_3^-, $H_2PO_4^-$, SO_4^{2-}, Fe, Mn, Al, Cu, Zn, B, Cd and Pb).

Soil Properties

Three sub-samples from the remaining peat cores collected for extractable nutrient pools were used to determine the organic content of each site, following loss on ignition methods adapted from Dean (1974):

$$\% \text{ Organic Content @ } 550^{\circ}C = \frac{\text{dry mass} - \text{ash mass(g)}}{\text{dry mass (g)}} \times 100\% \qquad (11)$$

Sub-samples from the remaining cores were also used to determine total C:N ratios using a Thermo Finnigan-Delta plus elemental analyzer-isotope ratio mass spectrometer (EA-IRMS) at the Environmental Isotope Laboratory, Dept. of Earth Sciences, University of Waterloo, ON. Additional cores from JACOS (1507 cm^3), POP and PAC (1963 cm^3) and WR N were used to determine bulk densities, specific yield and porosity using standard techniques (cf. Branham, 2012; Goetz, 2014; Silins and Rothwell, 1998, as cited in Redding and Devito, 2005)

Environmental Variables

Micrometeorological stations were set up at each study site, where air temperatures at a height of 1m were recorded every 30 min (HOBO; Onset) at WR, POP and PAC and air temperature at a 2 m height were recorded at 30 minute- intervals at JACOS. Peat temperatures at 2, 5 and 10 cm depths (copper constantan thermocouples) were recorded at 30-minute intervals throughout the peak-growing season and peat moisture at $0 - 25$ cm depth (Cs616 TDR; Campbell Scientific) was also recorded over 30 minute intervals at the JACOS site, and at 2.5, 7.5, 12.5, 17.5 and 22.5 cm depths at POP and PAC (Cs650 TRD; Campbell Scientific). No continuous moisture data were collected at WR, however manual measurements were recorded throughout the incubation period. Water table depth was measured every 30 minutes at WR D, WR N and POP and collected manually bi-weekly at JACOS and once a week at PAC. Precipitation was recorded using on site precipitation buckets at JACOS (RG3-M; Onset), POP, PAC (RGB-M002; Onset) and WR.

Additional measurements of peat temperature at 2 and 10 cm depths (thermistor probe; Omega) and the upper 7 cm of peat moisture (theta moisture probe; Delta T Devices) were taken manually throughout each three-week incubation, including the first and last day of each nutrient incubation. These data were then adjusted using an equation from a calibration curve with fitted gravimetric moisture data.

Statistical Analyses

Multiple linear regressions with microform and site (as independent factors) and nutrient dynamic (e.g. nutrient pools, net nutrient transformation rates or nutrient supply rates) were used to determine the interaction effects of spatial variations in nutrient dynamics

within and across peatlands. Additional linear regressions with just one independent factor (microform or site) were run to test for direct effects of microform or site on nutrient dynamics.

Kruskal Wallis tests were used to determine differences in climatic and environmental variables (e.g. precipitation, moisture, water levels, soil properties and mineral content) among sites and Mann-Whitney U tests were conducted to determine where these differences were among sites. All non-parametric tests were alpha corrected using a Bonferroni correction.

To determine the environmental drivers on nutrient dynamics across these systems, 2 types of regressions were ran: 1) multiple linear regression with water level, moisture and temperature as independent factors and a nutrient form (net transformation rates or nutrient supply rates) as the dependent factor. This regression tested for interaction effects; and 2) linear regression with one environmental variable as the independent factor and one nutrient form as the dependent factor. Both types of regressions grouped all sites together to determine the same key drivers of nutrient dynamics across all sites. To perform each regression, nutrient dynamics were transformed to meet all assumptions of multiple and linear regressions. Extractable NO_3^-, TIN, WEP and N supply rates were all transformed using a log function, net nitrification and N mineralization rates were transformed using a square root function and an inverse function was used to transform P supply rates.

Results

Climate data and Environmental Variables

The study season was an overall warm, wet season in comparison to 30-year climate records for the Fort McMurray region. Average daily air temperatures across the studied sites ranged from 17.8 to 19.3^{o}C, which is higher than the 30-year average for the region (15.5^{o}C).

All five sites received greater precipitation rates for the month of July relative to the region's climate normal (96 mm) where precipitation ranged from 247 to 104 mm. Mann-Whitney U tests with Bonferroni corrections determined that PAC had significantly larger precipitation events throughout the month of July than the other sites (p values < 0.05). Consequently PAC had significantly wetter conditions, which were apparent in greater peat moisture content (median (Mdn) 33 to 88% in hummocks and hollows, respectively) relative to the other peatlands studied (Mdn 20 and 46%, p values < 0.005 in hummocks and hollows, respectively) (Figure 4.2).

As expected, the peatlands fell along a hydrologic gradient. Conditions were dry at the WR (bog) sites, and wet at the JACOS and PAC (fen) sites. The POP site (fen) represented an intermediate between the dry bogs and wet fen sites, with dry hummocks (similar to WR sites) and wet hollows (similar to JACOS and PAC sites). Spatial variation in peat moisture was also observed within sites, where a threshold in moisture differences between microforms was observed at POP site (Figure 4.2). At the drier sites (WR) peat moisture contents were similar between microforms, however as peatlands became wetter, greater differences in moisture between microforms were observed as hollows were wetter than hummocks within the fen sites (Figure 4.2). Hereinafter, sites are organized following the moisture gradient from dry to wet.

Water table positions within the sites also demonstrated an apparent wetness gradient across the sites. Water levels were lowest at the WR site (108 cm below the surface in the drained section, 37 cm below the surface in the natural section) and the PAC site had the highest average water table, at 3.2 cm below the surface. All five sites had significantly different water table positions ($H(4) = 98.260$, $p < 0.001$, Figure 4.2).

Soil Properties

In general, soil properties were comparable among the bogs (WR D and WR N) and poor fens (JACOS and PAC); however, the rich fen (POP) had peat characteristics that differed from the other four sites. For example, peat within the POP fen (rich fen site) had a significantly lower organic content (81%) than peat found at WR N ($U = 0.000$, $p = 0.005$), JACOS ($U = 0.000$, $p < 0.001$) and PAC ($U = 0.000$, $p < 0.001$). At the other sites, significant differences in organic content were not found along the moisture gradient; however, significant differences were observed between the driest and wettest sites WR D (90% O.M.) and PAC (99% O.M.) ($U = 1.000$, $p = 0.006$) (Table 4.1). POP had a comparable C:N ratio to WR D bog ($U = 3.000$, $p = 0.157$) but had a significantly lower C:N ratio than WR N bog ($U = 2.000$, $p = 0.003$), and the poor fens JACOS ($U = 8.000$, $p = 0.001$) and PAC ($U = 0.000$, $p = 0.003$) (Table 4.1). The average bulk densities suggest that POP had relatively high bulk density in comparison to the other study sites (Table 4.1).

Geochemical Gradients Across Sites

Plant root simulator probes (PRS probes) were used to determine if minerotrophic and redox gradients existed among the peatland types. Calcium (Ca), potassium (K),

sulphur (S), iron (Fe) and manganese (Mn) supply rates did not increase along the moisture gradient (Figures 4.2, 4.3). Observed trends suggest that Ca, K and S concentrations were comparable among the bog sites (WR D and WR N) and the JACOS and PAC fens, where the median range of Ca fell between 145 and 220 mg/m^2/3 weeks, K had a median range of 51 to 77 mg/m^2/3 weeks and the median range of S was 10 to 16 mg/m^2/3 weeks. In contrast, the POP site (intermediate soil moisture) had the greatest Ca and S supply rates with median concentrations of 72 and 388 mg/m^2/3 weeks. However, K concentrations were low at the POP fen, with a median concentration of 65 mg/m^2/3 weeks (Figure 4.3). The POP fen was also somewhat unique from the other sites as it hosted significant tree cover (*Populus* spp.) relative to other sites (*Sphagnum* and vascular plants). In this paper, the POP site is hereinafter referred to as a rich-fen and the JACOS and PAC sites are referred to as poor fens.

Iron and Mn concentrations were used to infer the presence of absence of anoxic conditions at the sites. The majority of the study plots sampled across each peatland type had Fe and Mn supply rates lower than 20 mg/m^2/ 3 weeks. Elevated supply rates were not found in the hummocks at any of the sites. However, elevated Fe and Mn concentrations were observed in some hollows at the POP and JACOS sites, suggesting that several hollows sampled within these peatlands were anaerobic, acidic and had low redox (Western Ag. Innovations, 2014). These elevated supply rates were found in hollows with the highest peat moisture contents. Elevated Fe and Mn supply rates were not observed in the hollows at the dry WR sites, suggesting that these sites were aerobic.
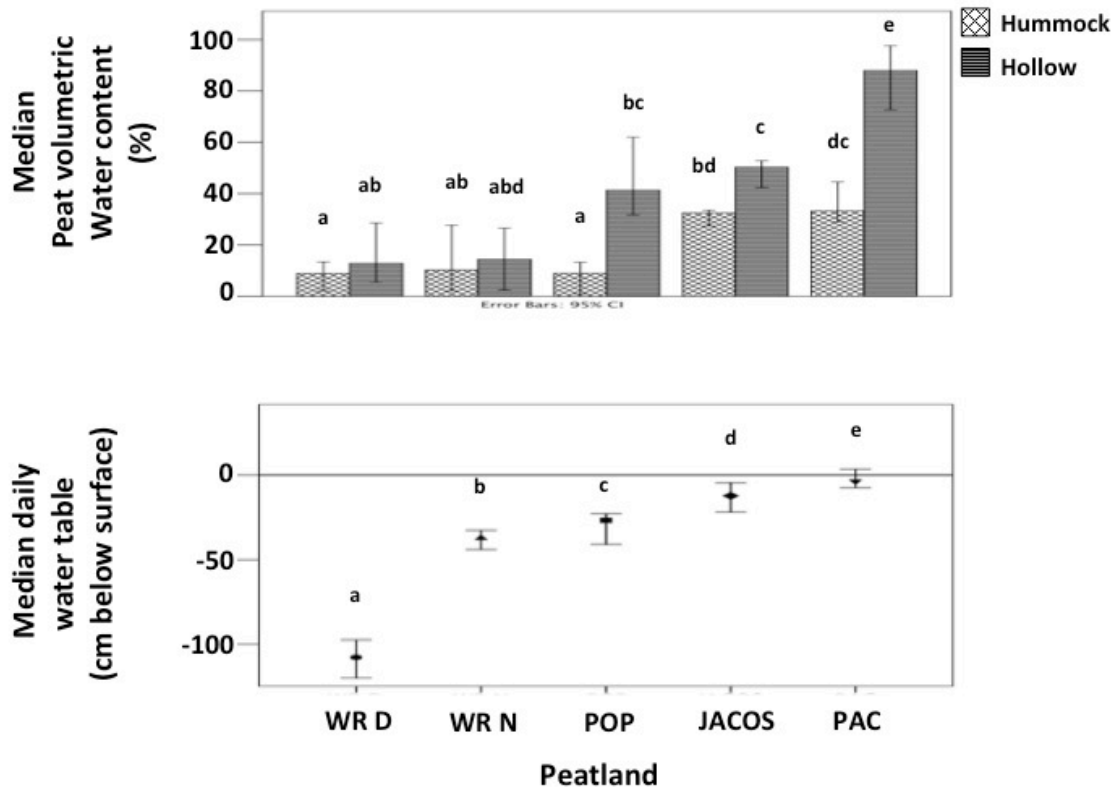
Figure 4.2: Comparison of peat volumetric water content (top figure) and median daily water table (bottom figure) across five different peatland types (x-axes) throughout the peak-growing season in 2012. Median peat moisture of hummocks and hollows of each site are depicted by bars, where light hatched bars show hummocks and dark horizontally lined bars depict moisture in hollows. The median daily water table for each peatland type is depicted by a corresponding symbol, having lines connecting to the maximum and minimum water table position observed over the peak-growing season. Differences in peat moisture and water table position were determined using Man-Whitney U tests and results are noted by lettering above each bar.

Table 4.1: Soil properties of five different peatland types in WBP of AB, where the median bulk density, porosity, specific yield, organic content and C:N ratio are provided.

Peatland	Soil Property					
	Depth (cm)	Bulk Density (g cm^{-3})	Porosity	Specific Yield	Organic Content (%)	C:N ratio
WR D	N/A	N/A	N/A	N/A	90 ± 7	48 ± 13
WR N	3-8	0.046 ± 0.014	N/A	N/A	99 ± 2	71 ± 23
	23-28	0.053 ± 0.005				
POP	0-5	0.017 ± 0.005	0.99 ± 0.00	0.78 ± 0.06	81 ± 10	32 ± 13
	5-10	0.079 ± 0.041	0.95 ± 0.03	0.44 ± 0.14		
	10-15	0.120 ± 0.023	0.91 ± 0.02	0.25 ± 0.15		
	15-20	0.144 ± 0.009	0.9 ± 0.02	0.14 ± 0.04		
	20-25	0.163 ± 0.005	0.88 ± 0.02	0.08 ± 0.02		
	25-30	0.147 ± 0.007	0.89 ± 0.02	0.08 ± 0.00		
JACOS	0-5	0.016 ± 0.013	0.99 ± 0.01	0.26 ± 0.09	97 ± 2	71 ± 18
	5-10	0.040 ± 0.032	0.97 ± 0.02	0.18 ± 0.03		
	10-20	0.086 ± 0.050	0.94 ± 0.03	0.14 ± 0.04		
	20-30	0.070 ± 0.065	0.95 ± 0.04	0.14 ± 0.04		
PAC	0-5	0.012 ± 0.002	0.98 ± 0.00	0.62 ± 0.07	99 ± 2	78 ± 8
	5-10	0.019 ± 0.008	0.97 ± 0.01	0.60 ± 0.11		
	10-15	0.034 ± 0.034	0.96 ± 0.02	0.38 ± 0.21		
	15-20	0.048 ± 0.012	0.94 ± 0.01	0.20 ± 0.10		
	20-25	0.062 ± 0.005	0.95 ± 0.01	0.12 ± 0.03		
	25-30	0.071 ± 0.004	0.94 ± 0.01	0.12 ± 0.02		

All soil properties are shown with ± SD. Organic content and C:N ratio were determined at the University of Waterloo, where sample sizes for organic content were as follows: WR D N = 4, WR N N = 4, POP N = 10, JACOS N = 21 and PAC N = 11. C:N ratios had sample sizes of N = 2, 6, 9, 14 and 5 for WR D, WR N, POP, JACOS and PAC, respectively. Bulk density of WR N was determined at the University of Calgary with an N = 6 and bulk density, porosity and specific yield of POP, PAC and JACOS were determined at the University of Waterloo, where POP and PAC had an N = 2 and JACOS N = 6.

Spatial Variability in Nitrogen Cycling

Spatial variability in N dynamics was found throughout the landscape. Extractable TIN and NO_3^-, supply rates and transformation (net N mineralization and net nitrification) rates were examined as a function of peatland (site) and microform (hummock, hollow). Median concentrations of TIN pools fell between 18 to 38 µg/g (all values expressed as

concentrations per dry mass of peat) in hummocks and 18 to 43 µg/g in hollows across the suite of peatlands. The two bogs (WR D and WR N) had lower TIN pools relative to the other peatlands, and results suggested that ext-TIN pools differed with peatland type (R^2 = 0.216, p = 0.001; Figure 4.4a). Hummocks at the POP site also had low TIN pools that were similar to those found at the WR N and WR D sites, which is similar to the observed differences in soil moisture across the sites (Figure 4.2, Figure 4.4a). NO_3^- pools were also found to vary with peatland type, although this did not occur along the moisture gradient as observed for TIN (R^2 = 0.300, p < 0.001; Figure 4.5a). Indeed, NO_3^- pools were slightly elevated in the hollows at the POP site (rich fen, Figure 4.5) and both hummocks and hollows at the WR N and WR D (bog) sites; however, the JACOS fen had extremely high NO_3^- pools relative to the other peatland types (*Mdn* 16 and 11 µg/g in hummocks and hollows, respectively), whereas all other peatland types had median ext-NO_3^- pools that ranged from 1 to 3 µg/g in hummocks and hollows. Linear regressions examining differences in TIN or NO_3^- pools with microform did not find significant relationships. A similar spatial distribution in net N mineralization rates was found across the peatlands, but was the reverse of what was found for TIN pools. Net N mineralization was observed at the dry sites (WRD and WRN and hummocks in the POP fen) but N immobilization rates (or lower net N mineralization) were observed at the wetter sites (POP hollows, JACOS, PAC). This spatial pattern was not observed for NO_3^- transformations, as net nitrification was observed at the WR, POP and PAC sites (*Mdn* 8 to 19 µg/g/month in hummocks, 5 to 10 µg/g/month in hollows) but strong net immobilization of nitrate was observed at the JACOS site (*Mdn* -22 µg/g/month in hummocks and -13 µg/g/month in hollows; Figure 4.5b). No clear differences between microforms were observed for either

net N mineralization or net nitrification at the sites, and no significant relationships were found for TIN (R^2 = 0.016, p = 0.353) or NO_3^- (R^2 <0.001, p = 0.890) transformations with microform type. Moreover, peatland type and microform were not significant factors in net N mineralization rates (R^2 = 0.063, p = 0.174), or net nitrification rates (R^2 = 0.019, p = 0.581).

Spatial patterns in N pools (Figures 4.4a, 4.5a) and transformation rates (Figures 4.4b, 4.5b) were not clearly reflected in N supply rates as indicated by PRS probes (Figures 4.4c, 4.5c). TIN supply rates (Figure 4.4c) were elevated at the JACOS and PAC sites (as was observed for TIN extractable pools at the onset of the three week period), but this was not observed in the hollows of the POP site. TIN supply rates (Figure 4.4c) were lower at the drier sites as was observed for TIN extractable pools (Figure 4.4a). NO_3^- supply rates were elevated at the WR D and WR N (bog) and JACOS sites relative to the POP and PAC fens (Figure 4.5a). Indeed, with the exception of the JACOS site, NO_3^- supply rates appeared to decrease across sites as moisture conditions increased. N supply rates were largely comparable between microforms within the sites with some exceptions. There was a significant interaction effect between microform and site on TIN supply rates (p = 0.017), where spatial variations were driven by moisture differences between microforms within the wetter sites (e.g. JACOS and PAC; Figure 4.2a) as hollows had greater TIN supply than hummocks. Significant relationships were not found between peatland type, microform and NO_3^- supply rates (R^2= 0.063, p =0.156) (Figure 4.5c).
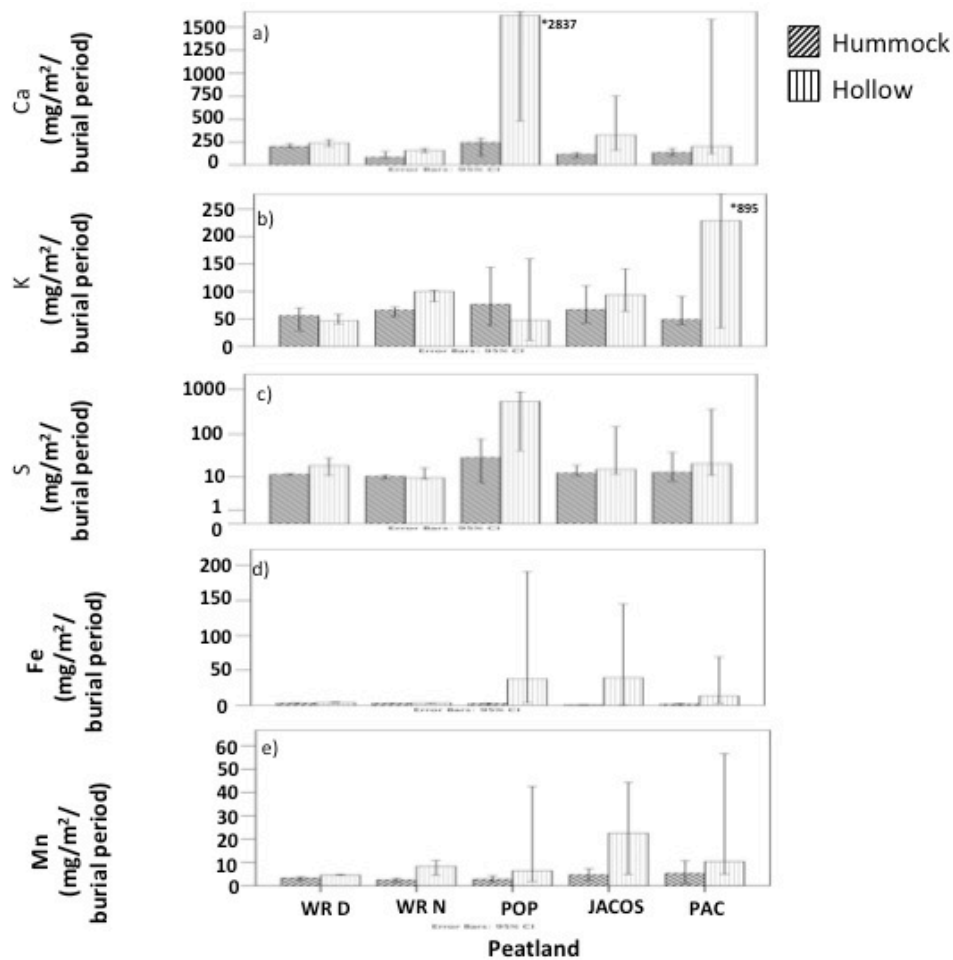
Figure 4.3: Comparison of mineral supply rates across five different peatland types in the WBP. The mineral supply rates include (a) calcium, (b) potassium, (c) sulphur, (d) iron, and (e) manganese. Supply rates (y-axes) were determined by PRS probes over 3-week burial periods throughout the peak growing season in 2012. The bars with diagonal lines are supply rates of hummocks and the bars with vertical lines show the supply rates of hollows.

Spatial Variability in Phosphorus dynamics

Water extractable PO_4^{3-} (WEP) pools ranged from <0.001 to 18 µg/g in hummocks and <0.001 to 48 µg/g in hollows. WEP pools did not vary with peatland type ($R^2 = 0.02$, $p = 0.753$; Figure 4.6a), but WEP pools in hollows were elevated relative to hummocks ($R^2 = 0.086$, $p = 0.025$) at most sites with the exception of the WR D site. WEP pools in the hollows at the JACOS fen were exceptionally high relative to the other sites (Figure 4.6a). WEP pools did not vary significantly when peatland and microform were tested together ($R^2 = 0.088$, $p = 0.079$). The combined effect of microform and peatland type on net P mineralization rates was also weak, explaining only 13% of the observed variation in P mineralization rates ($R^2 = 0.126$, $p = 0.026$; Figure 4.6b). Net P mineralization rates varied with peatland type ($p = 0.018$) but this variation was related to moisture differences in microtopography. For example, the drier sites (WR D, WR N and POP) had net P mineralization rates between *Mdn* 13 to 27 µg/g/month in hummocks, which is greater than what was observed in the hummocks at the wetter sites (JACOS and PAC), (*Mdn* net P mineralization rates -0.3 to 1 µg/g/month (Figure 4.6b). No differences in *Mdn* net P mineralization rates in hollows were found across the peatlands. However, net P mineralization rates were highly variable, where some high net P mineralization rates were observed in hollows at the WR D, WR N and JACOS sites (Figure 4.6b).

Phosphorus supply rates (as indicated by PRS probes) were highly variable in the landscape (0.5 to 2.5 mg/m^2/ month in hummocks and 0.1 to 2.4 mg/m^2/month in hollows), and did not show clear patterns. No statistical effect of peatland type or microform type was found ($R^2 = 0.053$, p values > 0.05). Supply rates of Fe and Mn were also included as indices of anoxic conditions.

Figure 4.4: The dynamics of (a) ext-TIN, (b) net N mineralization rates, and (c) TIN supply rates within and among five different peatland types in the WBP. White box plots show TIN concentrations in hummocks and the dark box plots represent TIN concentrations in hollows. Different peatland types are along the x-axes following a moisture gradient from dry to wet.
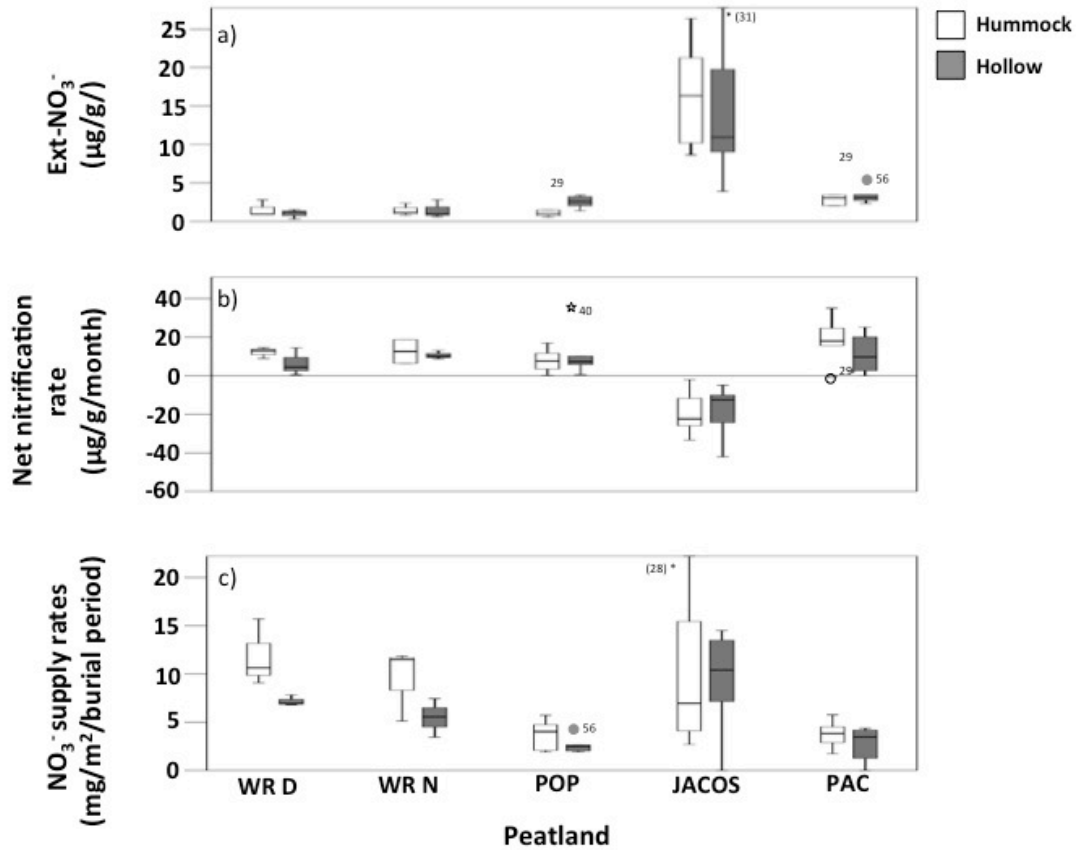
Figure 4.5: Nitrate cycling within and among five different peatland types in the WBP. (a) Ext-NO_3^-, (b) net nitrification rates, and (c) NO_3^- supply rates were analyzed to determine spatial differences in NO_3^- dynamics (y – axes) between microforms within and among study sites. White box plots represent hummocks and the dark box plots are hollows. The different peatland types are shown on the x axes, following a moisture gradient from dry to wet.

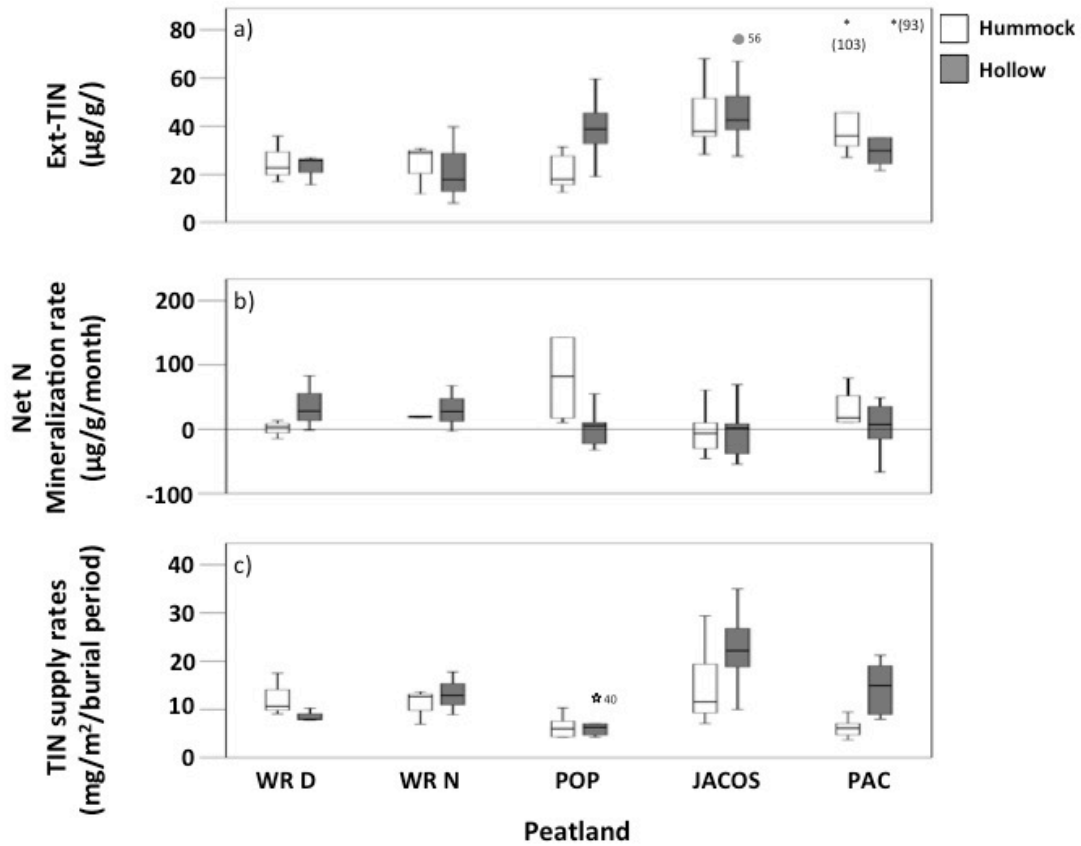**Figure 4.6**: The dynamics of (a) WEP, (b) net P mineralization rates, and (c) P supply rates within and among five different peatland types in the WBP. White box plots show P concentrations in hummocks and the dark box plots represent P concentrations in hollows. Different peatland types are along the x-axes following a moisture gradient from dry to wet conditions.
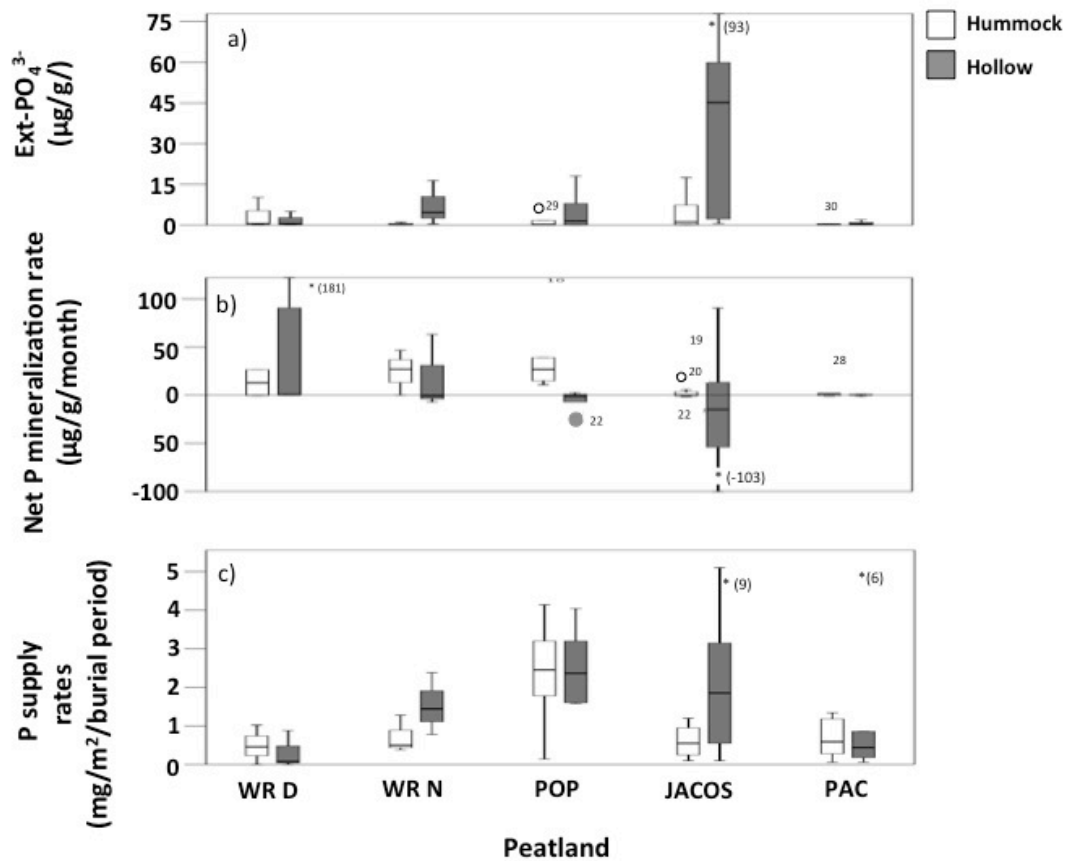
Effects of Environmental Variables on Nutrient Dynamics

The effects of soil moisture, water table position, temperature and anoxia (as indicated by Fe and Mn supply rates in PRS probes) on nitrogen and phosphorus transformation (mineralization) and supply rates, both together and independently were examined. Significant relationships (p <0.05) were found between soil moisture and net N and P mineralization but not net nitrification rates (Table 4.2). In contrast, net nitrification and net P mineralization rates were positively related to soil temperature (Table 4.2, $R^2 = 0.336$ & 0.108, p values <0.05, respectively). Multiple linear regressions with peat moisture, water table and temperature produced significant relationships with net nitrification ($R^2 = 0.248$, $p = 0.018$) and P mineralization ($R^2 = 0.206$, $p = 0.016$; although these were driven by soil moisture content).

Significant relationships were also found between net P mineralization and Fe x Mn supply rates (Table 4.2). Nutrient supply rates were largely driven by the same environmental variables as mineralization rates (Table 4.2), although some differences were observed. For example, both TIN and NO_3^- supply rates were significantly related to soil moisture, water table level and temperature ($R^2 = 0.244$ & 0.248, $p = 0.004$ & 0.003, respectively). In contrast, P supply rates were related to Fe and Mn supply rates (together, where Fe was the main driver), but not soil moisture or temperature (Table 4.2).

Discussion

Nitrogen and Phosphorus Content in WBP peatlands

Nutrient pools, transformations and supply rates were examined over a one-month period during the peak growing season across a range of peatlands in the WBP, with the goal of providing baseline data to inform reclamation work on disturbed peatlands in the region.

The peatlands represented an apparent moisture (and possibly minerotrophic) gradient, and included two bogs (one drained, one natural) and three fens (with varying vegetation and disturbance types). N and P concentrations in this study were slightly higher than those at other peatlands across the WBP (e.g. Wray and Bayley, 2008). However, this may be related to the fact that previous studies provided seasonal values (e.g. Wray and Bayley, 2008) whereas the current study focused on peak-growing season, when expected rates of mineralization and available nutrients would be at a seasonal high. It is notable that one site, JACOS fen had anomalously high extractable NO_3^- and WEP as well as high NO_3^- and P supply rates relative to the other sites along our moisture gradient (Figures 4.4 to 4.6). These elevated concentrations were not a result of higher net N or P mineralization (or nitrification) at the sites (Figures 4.4b to 4.6b). The JACOS fen is situated on Steam Assisted Gravity Drainage (SAGD) oil sands site composed of decommissioned well pads, which were located adjacent to several of the study plots. The development or installation of well pads has been found to contaminate nearby peat with oil and/or excess mineral content (Graf, 2009), which could have caused an influx of NO_3^- and/or P at the JACOS site that was not observed at the other peatland sites. The net immobilization rates and relatively high available nutrients suggest that there was rapid microbial uptake within JACOS that was not observed at the other peatland types. This suggests that JACOS is somewhat atypical from the other, peatlands along our gradient, and is most likely related to the elevated nutrient pools determined on the north side of the road, where an external supply of N and P (e.g. well pads and/or ash from a past fire) is driving nutrient cycles.

Effects of a Hydrologic Gradient on N and P Dynamics

A gradient in water positions were found across the peatlands, but did not translate to a gradual increase in soil moisture over the one-month study period (Figure 4.2). The limited differences in soil moisture across sites were most likely an effect of the sub humid climate and high evapotranspiration rates in the WBP (Solondz *et al.,* 2008) and capillary action. However, an apparent moisture threshold between dry sites (two bog sites and hummocks at POP site) and wet sites (hollows at POP and JACOS, PAC sites) was found. Redox conditions followed the moisture threshold, with elevated Fe and Mn supply rates at the very wet sites (Figures 4.2, 4.3); however, this was limited to the hollows and was not observed in hummocks at any of the sites.

Net N and net P mineralization rates were elevated at the dry sites (WR D, WR N and POP hummock) relative to the wet sites (POP hollow, JACOS, PAC) (Williams and Wheatly, 1988; Holden *et al.,* 2004). However, this is in contrast to extractable nutrient pools, which appeared to be greater at wetter sites. This contradicts findings from previous studies, where a lowering of the water table triggered net N mineralization and increased ext-TIN pools (Williams and Wheatley, 1988; Holden et al., 2004). The finding that TIN pools did not increase with net N mineralization, and instead increased with moisture conditions (where net N mineralization was suppressed) could be due to an influx of nutrients from groundwater in the fens as groundwater has been found to supplement available N in fens (Walbridge and Navarathnam, 2006). This is supported by data collected at the JACOS site (not shown) that showed elevated N concentrations in shallow groundwater. The finding also suggests that nutrient pools were driven by external sources of N and not by internal processes (mineralization and decomposition).

Spatial variation in ext-NO_3^- was comparable within and among peatland types, with the exception of JACOS where ext-NO_3^- pools were extremely high. Net nitrification rates were linked primarily with peat temperature rather than moisture conditions. However, this contradicts a recent study looking at the effects of water table draw down on N dynamics, where a water table draw down of 20 cm had a negative effect on net nitrification rates (Macrae *et al.,* 2013).

Extractable PO_4^{3-} (WEP) and P supply rates were related to moisture conditions but unlike, ext-TIN, WEP and P supplies did not follow a general moisture gradient across the sites, but instead increased with sites having low redox conditions. These conditions were found in hollows at sites (POP and JACOS) having elevated Fe and Mn concentrations (as determined by PRS probes). Elevated concentrations of available P in peat having low redox is not an unusual finding; Richardson and Marshall (1986) determined that peatlands having flooded, low redox and anoxic conditions have an excess release in P through a reduction process where ferric Fe (Fe^{3+}) transforms to Fe^{2+} and P becomes unbound from oxyhydroxide flocs in the soil (Aldous *et al.*, 2005). In contrast to this, net P mineralization rates were not effected by redox but had an inverse relationship with moisture, where the drier sites (the two bogs at WR and fen at POP) had net mineralization compared to the two wettest sites (JACOS and PAC), which had net

Table 4.2: Environmental controls on peat nutrient concentrations in upper 10 cm peat

Nutrient Form with Variables	R^2	Sig[a]
Net N mineralization (µg/g/month)		
θ *WT* T2*T10	0.119	0.143
θ	0.073	**0.035**
WT	0.034	0.169
T2	0.030	0.191
Fe*Mn	0.019	0.595
Net nitrification (µg/g/month)		
θ *WT* T2*T10	0.248	**0.018**
θ	0.012	0.420
WT	0.046	0.106
T2	0.336	**< 0.001**
Fe*Mn	0.032	0.407
Net P mineralization (µg/g/month)		
θ *WT* T2*T10	0.206	**0.016**
θ	0.111	**0.012**
WT	0.068	**0.049**
T2	0.108	**0.013**
Fe*Mn	0.124	**0.028**
TIN supply rates (mg/m^2/3 weeks)		
θ *WT* T2*T10	0.244	**0.004**
θ	0.075	**0.035**
WT	0.019	0.287
T2	0.156	**0.002**
Fe*Mn	0.026	0.472
NO$_3^-$ supply rates (mg/m^2/3 weeks)		
θ *WT* T2*T10	0.248	**0.003**
θ	0.018	0.312
WT	0.032	0.177
T2	0.071	**0.044**
Fe*Mn	0.051	0.237
P supply rates (mg/m^2/3 weeks)		
θ *WT* T2*T10	0.013	0.947
θ	<0.001	0.896
WT	0.006	0.570
T2	0.002	0.718
Fe*Mn	0.138	**0.014**

Results from regressions with peat nutrients and peat moisture (θ), water table position (WT; cm below surface), peat temperature at surface (T2; 2 cm below surface) and 10 cm below the surface (T10; ^{o}C), and iron (Fe) and manganese (Mn) supply rates (mg/m^2/3 weeks).
[a]Results significant at the 0.05 level are in bold

immobilization. This is to be expected as mineralization has been found to increase with aeration (Walbridge and Navaratnam, 2006) and similar results have been found in other studies (Bridgham *et al.*, 1998). These results suggest that P dynamics are similar across different types of peatlands but vary with differences in redox within and across peatlands.

Effects of a Minerotrophic Gradient on Nutrient dynamics

The gradient in soil moisture across the studied sites was not reflected in a gradient in mineral supply rates, as mineral supply rates were comparable among the dry (bog) sites and wettest "poor" fen sites (JACOS, PAC) and elevated at the POP site (intermediate soil moisture conditions, greater vegetation diversity and abundance (rich fen). Nutrient concentrations in the rich fen (POP) were not different from the other peatlands in our study, suggesting that N and P pools do not vary with peatland minerotrophic conditions, a finding not uncommon in more recent peatland studies (Bridgham *et al.*, 1998; Verhoevan *et al.*, 1990; Kellogg and Bridgham, 2003). N and P dynamics were driven by moisture conditions, suggesting that in this landscape, N and P dynamics appear to be more related to environmental conditions such as moisture or temperature and groundwater nutrients rather than differences in mineral content.

Conclusion and Implications for Reclamation Practices

Nutrient dynamics (N and P) did not vary among different peatland types along an ombrotrophic-minerotrophic gradient, where bogs, poor fens and rich fens had comparable nutrient contents. Spatial variations in N and P within peatlands were weakly

related to the natural variation in microtopography at some sites, and were largely driven by environmental variables such as peat moisture, water table position and temperature. However, the effects of these factors on N and P dynamics differed. Extractable TIN and N (TIN and NO_3^-) supply rates followed a moisture threshold, where TIN (pools and supply rates) increased with moisture and NO_3^- supply rates declined with moisture content. The elevated concentrations of ext-N and N supply rates across the sites did not coincide with net mineralization and nitrification rates, as transformations rates were similar across the sites. This suggests that external processes were the drivers in N dynamics within these systems and that the moisture threshold was not large enough to cause spatial differences in N content. Phosphorus cycling did not share the same trends as N dynamics, where P dynamics were indirectly affected by moisture and driven by redox conditions, in hollows when conditions were anoxic.

Exceptions to the general findings were observed at one peatland (JACOS), which had decommissioned well pads as well as left over ash from a past fire and was bisected by a semi-permanent road. Nitrate and P availability within this site were extremely high in comparison to all other peatland types studied. This suggests that peat in contact with these types of industry related disturbances could become contaminated resulting in significantly greater nutrient concentrations than their natural functioning counterparts.

The study suggests that future research should focus on temporal variations of nutrient dynamics among different peatland types to gain a better understanding of how these peatlands function and how they vary annually and seasonally. Furthermore, we suggest that future reclamation practices focus on controlling hydrology (moisture and

water table position) to ensure nutrient dynamics are similar to those found in the natural environment. Additionally, the peat being used to reclaim mined areas, should be sourced from an undisturbed site, as peat that has been in contact with well pads and gravel roads could have excessive nutrients which have the potential to shift vegetation and microbial communities over time.

Chapter 5

Conclusions and Recommendations

Spatio-Temporal variations in N, P and CO$_2$ dynamics in a poor fen

The first objective of this thesis was to determine temporal and spatial variations in N, P and CO$_2$ dynamics of a poor fen in the AOS. The findings suggest that both external (groundwater) and internal (mineralization) sources supply nutrients to peat throughout the growing season. However, N (NO$_3^-$ and NH$_4^+$) and P dynamics do not follow the same spatio-temporal trends and instead, N and CO$_2$ shared similar seasonal dynamics.

N and CO$_2$ varied seasonally with temperature and plant growth, where Ext-N pools and productivity (GEP) increased throughout the season (June to August). Net N transformation rates (net mineralization and nitrification) and N supply rates also varied seasonally as N mineralization and nitrification peaked in late June to mid July (Incubation Period 2) and N supply rates declined from early June to mid July (Periods 1 and 2) and later peaked in late July to August (Period 3).

Although N and CO$_2$ followed similar seasonal trends, we did not find any significant relationships between the two, which could be a result of the difficulty in characterizing true relationships among the inter-couplings with N, C and their biotic and abiotic factors.

P supply rates were the only form of P that varied seasonally, where supply rates declined with vegetation growth. Supply rates differed from WEP, as supply rates estimate the surplus of nutrient content after plant and microbial uptake. WEP, on the

other hand were determined using peat cores free of live vegetation, eliminating the plant uptake of P. However, both WEP and supply rates did vary spatially, reflecting differences in moisture and redox conditions between microforms. The wetter microforms (hollows) were found to have greater release of available P resulting in larger WEP and P supply rates than the drier hummocks.

Moisture differences between hummocks and hollows also had a biogeochemical (yet statistically insignificant) effect on respiration, where a threshold of moisture (> 45%, only observed in hollows) decreased respiration rates.

Nutrient Dynamics among and within peatlands in the WBP

Spatial variation in nutrient (N and P) content across a range of peatland types in the AOS was limited, suggesting that available N and P concentrations did not follow a geochemical (minerotrophic-ombrotrophic) gradient and instead were driven by environmental variables and a slight moisture threshold. However, the drivers in N and P dynamics differed, where, ext-TIN and N supply rates (TIN and NO_3^-) followed a moisture threshold where TIN supply rates increased with wetter sites whereas supply rates decreased with moisture. Net N transformation rates were comparable across peatlands and the moisture threshold suggesting that N pools and supply rates were driven by external factors such as groundwater N, moisture, water table position and temperature. These factors were also related to the few spatial differences observed within peatlands.

P dynamics were controlled by redox, where sites having low redox and anaerobic conditions had greater P content. These conditions were only found in hollows of the

wettest peatlands studied (the rich fen and two poor fens) and resulted in P availability to be greater in hollows than hummocks within these sites.

Effects of a linear disturbance on nutrients and CO$_2$ dynamics

The construction of a semi-permanent road on a poor fen (JACOS) had a significant impact on the hydrology of the system, dividing the fen into "wet" (greater peat moisture and high water table position) and "dry" (lower peat moisture and water table level) sections. However, the change in hydrology only had marginal effects on nutrients (NH$_4^+$ and NO$_3^-$) within the fen. Suggesting that a threshold in moisture was not reached in order to affect net N transformation rates, N supply rates and CO$_2$ exchange. Additionally, many of the biotic and abiotic drivers of terrestrial CO$_2$ exchange were the same on the wet and dry side of the fen resulting in insignificant differences in CO$_2$ flux rates (GEP and R$_{tot}$) between the two sides of the fen.

Although, the road had marginal to no impacts on N and CO$_2$, the significant change to the site's hydrology could be impacting the vegetation community. It has been documented that mosses are particularly sensitive to changes in hydrology as they lack a root system (Clymo and Hayward, 1982, as cited in Graf, 2009) and shifts in the vegetation community may not be observed for several decades (Findlay and Bourdages, 2000). A slight shift in vegetation communities was observed at JACOS, where the drier side (north side) of the fen had less *Sphagnum* moss cover and the presence of lichen, which was not found on the wet (south side) side of the fen (Table 3.2, Chapter 3) and it is unknown how or if current and future changes in vegetation diversity will affect nutrient and CO$_2$ dynamics within the fen.

Contrary to the results from Chapter 3, results from Chapter 4 suggest that JACOS had abnormally high NO_3^- and P content compared to the other peatland types studied in the AOS. This is most likely a result of an atypical external source feeding nutrients to the JACOS ecosystem and could be caused by the leaching of mineral content used to develop the road and/or the caps well pads adjacent to the study plots. This finding suggests that the materials used in the development of roads and other disturbances have a greater effect on nutrient dynamics than the alteration to the local hydrology.

Suggestions to the Energy Sector on creating successful BMPs and Reclamation Projects

Our conclusions suggest that reclamation practices having the goal to construct a productive system post-disturbance do not have to focus on nutrient dynamics because nutrient dynamics do not appear to be directly related to vegetation productivity. However, if the goal is to restore the landscape to pre-disturbed conditions or to conserve natural biogeochemical and ecohydrological cycles then nutrient dynamics should be acknowledged in the decision making process. In these scenarios, we suggest that BMPs should reduce the contamination of peat throughout oil development and limit the alterations to local hydrology in order to preserve nutrient dynamics, CO_2 exchange and over the long-term, vegetation communities.

Many suggestions in reducing the effects of road and well pad construction on peatlands have been previously documented and include: (1) Construct roads parallel to the natural flow of water. (2) Create drainage systems allowing for the free flow of water.

(3) Use native materials for road construction to limit invasive species and contamination of peat. (4) The development of well pads should have drainage systems that collect runoff, reducing oil and mineral contamination of peat as well as the erosion of the well pad itself (B.C. Ministry of the Environment, 2008, as cited in Graf, 2009).

To reclaim post-disturbed sites with native vegetation, it has been suggested to remove the upper layers (acrotelm) of peat prior to the development of roads, well pads or mining. This prevents compaction and contamination of the vegetation, which can then be stored and used to reclaim decommissioned areas (Ryder *et al*., 2004, as cited in Graf, 2009).

Suggestions for Future Research on N, P and C dynamics in WBP

Future research should conduct a more complete nutrient and carbon study focusing on not only peat extractable nutrients, nutrient net transformation rates, nutrient supply rates and chamber terrestrial carbon flux rates but also determine leaching and gross mineralization of nutrients as well as ambient CO_2 fluctuations and determine carbon content found in peat and groundwater. Determining vegetation growth and nutrient uptake by plants would be useful in future studies to assess the relationship(s) between nutrients and CO_2. These studies should also be conducted over several seasons to better understand the inter-annual variability in N and C dynamics. Additionally, future research should look at these dynamics across a wider range of peatland systems having a more defined mineral and moisture gradient than the current study and include peatlands having a range of linear and non-linear disturbances to determine a more conclusive understanding of how energy development affects these delicate ecosystems over short

and long term time intervals.

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